Eesti Maaülikool
Estonian University of Life Sciences

THE DEVELOPMENT AND BIOMASS PRODUCTION OF GREY ALDER STAND ON ABANDONED AGRICULTURAL LAND IN RELATION TO NITROGEN AND CARBON DYNAMICS

ENDISELE PÕLLUMAALE RAJATUD HALL-LEPIKU ARENG, BIOMASSI PRODUKTSIOON JA LÄMMASTIKU- NING SÜSINIKU DÜNAAMIKA

JÜRGEN AOSAAR

A Thesis
for applying for the degree of Doctor of Philosophy in Forestry

Väitekiri
filosoofiadoktori kraadi taotlemiseks metsanduse erialal

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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following four original publications (I-IV). The articles are referred to in the text according to their Roman numerals.

I Uri V, Lõhmus K, Kiviste A, **Aosaar J** (2009) The dynamics of biomass production in relation to foliar and root traits in a grey alder (*Alnus incana* (L.) Moench) plantation on abandoned agricultural land. Forestry 82(1):61-74

II **Aosaar J**, Varik M, Lõhmus K, Uri V (2011) Stemwood density in young grey alder (*Alnus incana* (L.) Moench) and hybrid alder (*Alnus hybrida* A. Br.) stands growing on abandoned agricultural land. Baltic Forestry 17(2):256-261

III **Aosaar J**, Varik M, Uri V (2012) Biomass production potential of grey alder (*Alnus incana* (L.) Moench.) in Scandinavia and Eastern Europe: a review. Biomass & Bioenergy 45:11-26

IV Uri V, Lõhmus K, Mander Ü, Ostonen I, **Aosaar J**, Maddison M, Helmisaari, H-S, Augustin J (2011) Long-term effects on the nitrogen budget of a short-rotation grey alder (*Alnus incana* (L.) Moench) forest on abandoned agricultural land. Ecological Engineering 37:920–930

V **Aosaar J**, Varik M, Lõhmus K, Ostonen I, Uri V (2012) Long-term study of above- and belowground biomass and production in relation with soil nitrogen and carbon dynamics and accumulation in the grey alder (*Alnus incana* (L.) Moench) plantation on former agricultural land. European Journal of Forest Research (manuscript, submitted)

The contributions from the authors to the papers were the following:

Paper	Original idea and study design	Data collection	Data analysis	Preparation of the manuscript
I	VU, KL	VU, **JA**	KL, VU, AK	VU, KL, AK, **JA**
II	VU, **JA**	**JA**, VU, MV	VU, **JA**, KL	**JA**, VU, KL, MV
III	VU, **JA**	**JA**	**JA**, VU	**JA**, VU, MV
IV	VU, KL, ÜM	VU, **JA**, MM, HH, JAU	VU, KL, ÜM, IO	VU, KL, ÜM, HH, **JA**, IO
V	VU, **JA**	VU, **JA**, MV, HB	VU, KL, IO	**JA**, VU, KL, MV, IO

AK – Andres Kiviste, HB – Hardo Becker, HH – Heljä-Sisko Helmisaari, IO – Ivika Ostonen, **JA – Jürgen Aosaar**, JAU – Jürgen Augustin, KL – Krista Lõhmus, MM – Martin Maddison, MV – Mats Varik, VU – Veiko Uri, ÜM – Ülo Mander.

ABBREVIATIONS

AGB	Aboveground biomass
BGB	Belowground biomass
CAI	Current annual increment
CRB	Coarse root biomass
DBH	Diameter at breast height
DM	Dry matter
FOE	Foliar assimilation efficiency
FRB	Fine root biomass
FRE	Fine root efficiency
FRP	Fine root production
LAI	Leaf area index
MAI	Mean annual increment
NB	Nodule biomass
NNM	Net nitrogen mineralization
NPP	Net primary production
NUE	Nitrogen use efficiency
SLA	Specific leaf area
SRF	Short-rotation forestry

1. INTRODUCTION

In Estonia approximately half of the territory is covered with forest, grey alder stands forming 8.6% of the total forest area (Aastaraamat Mets 2010). During the last half century the increase of the forest coverage and growing stock has been continuous. According to Yearbook Forest 2010, the growing stock and area of grey alder stands in Estonia has been increasing continually for more than half a century, reaching up to 178,000 hectares and 31 million m^3, respectively (Aastaraamat Mets 2010). Beside the forest land, grey alder is known as a vigorous pioneer species which successfully occupies agricultural areas left out of use (Tullus *et al.*, 1998). A significant increase in the area of abandoned agricultural lands due to changes in the political and economic situation took place in Eastern Europe, including Estonia, at the end of the last century (Astover *et al.*, 2006; FAO, 2008; Henebry, 2009). In Estonia the area of abandoned agricultural land after the collapse of the USSR has increased drastically, reaching ~400,000 hectares (Estonian Rural Development Plan); the respective global estimate is 385 million to 472 million hectares (Campbell *et al.*, 2008). During the last decade the situation in Estonia has started to change; the area of abandoned arable holdings is gradually decreasing since they are brought back into agricultural use. However, a part of these areas represent a potential for growing fast- growing tree species, among them grey alder, as short-rotation forestry (SRF) plantations for producing energy wood. The SRF is regarded as a silvicultural practice employing high-density plantations of fast-growing tree species on fertile land (Weih, 2004). The favourable qualities of grey alder - rapid growth in juvenile age; high capability of biomass production; symbiotic nitrogen fixation capacity; wide natural distribution; frost hardiness; small number of damaging pests – make it a suitable tree species for SRF in Scandinavia and in the Baltic countries. Biomass production studies of grey alder have been carried out mostly by Scandinavian and Baltic scientists owing to the wide natural distribution of the species in this region. In Estonia, the growing stock of grey alder is 31 million m^3 (Aastaraamat Mets 2010); in Latvia 31 million m^3 (Miežite, 2008); in Lithuania 21 million m^3 (Forest statistics Lithuania 2009); in Sweden 49 million m^3 (Swedish statistical yearbook of forestry 2009).

Earlier studies have confirmed the high productivity of grey alder stands both on mineral and organic soils (Ovington, 1956; Granhall and Verwijst, 1994; Saarsalmi, 1995; Rytter, 1996; Lõhmus *et al.*, 1996; Telenius, 1999; Uri *et al.*, 2002, 2003, **I**). Hence, the agricultural land used for the cultivation of fast-growing tree species may become an important supplier of renewable energy which could contribute to the EU 20-20-20 strategy (Directive 2009/28/EC).

According to the grey alder yield-tables analyzed in paper **III**, the Baltic region is the most favourable for growing grey alder stands. However, the majority of yield-tables have been worked out quite a long time ago and, due to the changed growing conditions (drainage, increased atmospheric CO_2 level, increased annual temperatures, *etc.*), they may not reflect the present situation. As the economic importance of grey alder was considered limited in the past, there were compiled no recent grey alder yield-tables.

Today the resource of grey alder in Estonia is still managed to a modest extent. Yet in recent years there have been built several power plants and boiler houses operating on wood fuel. The nearest years will probably witness an increase of the bioenergy sector, which may stimulate more extensive use of energy wood as well as more extensive management of grey alder stands. As the economic value of grey alder timber has been low, earlier studies are practically missing and cultivated alder stands are very rare in Estonia. Hence, the demand for a new knowledge about the sustainable and environmentally friendly management of such stands will increase.

The present thesis is based on the results of a long-term research of a grey alder plantation growing on abandoned agricultural land. The plantation was established in 1995. It has been under continuous investigation during 17-years, which has made it possible to record the stand's growth dynamics as well as all changes in soil pH and carbon and in nitrogen dynamics. The long-term time series of the results make the research valuable since experiments employing similar approach are quite rare in the literature. The results of the study will allow giving silvicultural recommendations for landowners and other stakeholders for managing grey alder stands.

The working hypotheses of the present study were:

1. Grey alder stand on abandoned agricultural land is highly productive; the optimum rotation length for grey alder SRF stand is 15-20 years, which is the bulk maturity of the species;

2. The fine roots of alders affect significantly carbon and nitrogen cycling in stand;

3. Young grey alder stands act as a carbon and nitrogen sink and there is a strong positive impact to the soil fertility already in the early stage of stand growth;

4. Grey alder stand on former agricultural land is not a source of nitrogen hazard (leaching; N_2O emissions).

In the present dissertation various issues related to grey alder stands were studied:

In the silvicultural aspect, the dynamics of stand growth, the biomass production, the optimal stand density and the rotation length of the stand were analysed. As alders are able to introduce additional nitrogen into the ecosystem due to symbiotic N_2 fixation, more emphasis was given to environmental issues such as the nitrogen cycle and the carbon cycle. Several C and N fluxes and storages (net nitrogen minearlization; atmospheric N_2 fixing; N leaching into groundwater; N_2O emissions) were studied. The C sequestration into biomass (above- and belowground biomass) as well as into soil was estimated.

2. REVIEW OF THE LITERATURE

2.1. Aboveground biomass production of grey alder stands

Reports on biomass production are published on the basis of experiments conducted with different designs: plantation/natural stand; mineral/peat soil; thinned/unthinned stands; unfertilized/various fertilization treatments; stands of different ages; stands with widely ranging densities. According to reported results, grey alder has proved its capability for fast growth both on mineral soil and on peatland (Ovington, 1956; Granhall *et al.*, 1994; Saarsalmi, 1995; Rytter, 1996; Lõhmus *et al.*, 1996; Telenius, 1999), (Nagoda, 1966; Saarsalmi *et al.*, 1985; Hytönen *et al.*, 1995; Lõhmus *et al.*, 1996; Tullus *et al.*, 1998; Johansson, 1999, 2000; Rytter *et al.* 2000; Uri *et al.*, 2003, **I**; Miežite and Dreimanis, 2006) and is a promising tree species for SRF in Estonia (Uri *et al.*, 2002, 2003, **I**). Significant grey alder production values are reported from Sweden by Johansson (2000) where in the stand growing on former agricultural land at the age of 6-, 10- and 15-years the stem mass reached 21, 87 and 124 t ha^{-1}, respectively.

Abandoned agricultural areas are rapidly occupied by different pioneer tree species, among them grey alder. The growth of alders on former arable lands has been reported in many countries: Estonia (Uri *et al.*, 2002), Finland (Saarsalmi, 1985) France (Anthelem *et al.*, 2001), Korea (Lee *et al.*, 2002), Latvia (Liepins *et al.*, 2008), Norway (Staaland *et al.*, 1998), Russia (Shvidenko *et al.*, 1997), Sweden (Granhall *et al.*, 1994). Furthermore, alders are successfully used for the afforestation of mining areas (Helm and Carling, 1993; Lõhmus *et al.*, 2006).

There are several yield-tables available for grey alder: Latvia (Ozols and Hibners, 1927; Murnieks, 1950); Estonia (Raukas, 1930); Finland (Miettinen, 1933); Norway (Børset and Langhammer, 1966); Lithuania (Jankauskas) and Belarus (Yurkevich) (Krigul, 1971), which are compared more in detail in the review article (**III**). According to the yield-tables, the most productive young grey alder stands are growing in Latvia where stands stem volume at the age of 15- and 20-years is approximately 170 m^3 ha^{-1} and 200 m^3 ha^{-1}, respectively.

2.2. Stand density

The productivity of the stand depends largely on the number of stems per hectare and if stand density is low, it may limit biomass production since the trees can not realize the full potential of soil fertility. Despite the importance of stand density for biomass production, the issue has not been very thoroughly addressed by the researchers. Still, some results are reported by Johansson (1999, 2000). The question of the initial density of the plantation has been investigated by (Saarsalmi *et al.*, 1985; Hytönen *et al.*, 1995; Rytter, 1995; Uri *et al.*, 2002; Hytönen and Saarsalmi, 2009). Saarsalmi *et al.* (1985) carried out an experiment in a plantation with an initial density of 40,000 ha^{-1}. The study results reported from the plantation handled in the current thesis the initial density was 15,750 ha^{-1}.

Very few studies are available about precommercial thinnings. Rytter (1995) stated that during the 13-year period about the same amount of biomass was produced in the thinned and unthinned plantation growing on a dained sphagnum bog in central Sweden. Johansson (1999) claims if the alder stands should be managed for biofuels, no thinnings is needed, however, if a stand is used for timber production, one or two thinnings should be applied and removed stems could be used as biofuel. Daugavietis *et al.* (2009) reccomends thinning in a grey alder stand at the age of 3-5-years; the number of trees after thinning should be to 4,000-5,000 ha^{-1}.

2.3. Annual increment and rotation length

The mean and current annual increments (MAI and CAI, respectively) show the productivity of a stand. The MAI is calculated on the basis of the growing stock and stand age. The CAI shows the stand's current year productivity and depends on stand age and the weather conditions of a particular year. As estimation of CAI is time and labour consuming, the values of CAI reported in yield-tables or research papers are quite rare.

According to a conventional approach, decline in MAI indicates optimum time for harvesting a SRF stand. An optimal rotation length of 15-20 years is supported by several studies (Raukas, 1930; Björklund and Ferm, 1982; Rytter, 1995; Lõhmus *et al.*, 1996; Tullus *et al.*, 1998; Rytter *et al.*, 2000; Miežite and Dreimanis, 2006; Daugavietis *et al.*, 2009; **I**), which is in good accordance with the yield-tables reported in paper **III** where MAI of the most productive yield-tables at the age of 15- 20-years is in range of 4-5 t ha^{-1}. A few studies suggest a rotation length of up to 10 years (Rytter *et al.*, 1989; Johansson, 1999). Johansson (1999) suggested a rotation length of 40-50 years if good quality timber is aimed at.

The highest grey alder CAI value was reported by Granhall and Verwijst (1994) from a 5-year-old stand in Sweden which reached as high as 17 t ha^{-1} y^{-1}. In a study by Lõhmus *et al.* (1996) the CAI of a 14-year-old stand in Estonia was 8.3 t ha^{-1} y^{-1}. Eriksson and Johansson (2006) calculated the CAI of a 13-year-old grey alder stand growing in Central Sweden at 10.9 t ha^{-1} y^{-1}. Ample research on grey alder has conducted by Utkin *et al.* (1980) in Western Russia where the CAI values of 5-50-year-old stands ranged between 1.8-7.6 t ha^{-1} y^{-1}.

2.4. Wood density

For analysing the reported biomass results and comparing them with the data of yield-tables and, vice versa, a relevant wood density value is essential. The published grey alder wood densities are highly variable. The values reported by Nordic authors are quite low (Hakkila, 1970; Björklund and Ferm, 1982; Johansson, 2005) compared to the values reported from the Baltic countries (Table1; Table 3 in **II**). Only a few results can be found about grey alder wood density from Estonia (Keedus and Uri, 1997; **II**).

Table 1. Average stemwood densities of grey alder on the basis of different literature sources.

Country	Author	Density kg m^{-3}
Norway	Stemsrud, 1964	369
	Nagoda, 1966	365
	Vadla, 1999	340 (324-358)
Sweden	Johansson, 2005	359 (230-440)
Finland	Hakkila, 1970	361
	Björklund and Ferm, 1982	353
Estonia	Keedus and Uri, 1997	384
	Aosaar *et al.*, 2011 (**II**)	396
Latvia	Vanins, 1950	432-574
	Pirag, 1962	420
	Draudinš and Bekeris, 1979	420-630
	Klevinska and Bikova, 1999	432-458
	Miežite, 2008	447 (388-506)

2.5. Fine root and nodule biomass and production of grey alder

For estimation of fine root biomass (FRB) and fine root production (FRP), different methods are described by many authors: the sequential coring method (Ahlström *et al.*, 1988; Vogt and Persson, 1991; Helmisaari *et al.*, 2002), the ingrowth core method (Persson, 1983; Makkonen and Helmisaari, 1999; Brunner *et al.*, 2012) and the minirhizotron method (Majdi and Nylund, 1996; King *et al.*, 2002; Ostonen *et al.*, 2005). In recent years the root mesh method has been applied for estimation of FRP (Hirano *et al.*, 2009; Lukac and Godbold, 2010).

The research of FRB and FRP is very time- and labour consuming, only a few papers on the FRB and FRP of grey alder are available so far (Saarsalmi *et al.*, 1985; Rytter, 1989; Elowson and Rytter, 1993; Uri *et al.*, 2002, **I**). As a N_2 fixing tree species, with the nodules playing a crucial role in the functioning of its ecosystem, several studies have addressed this issue (Bond *et al.*, 1954; Akkermans and van Dijk, 1976; Johnsrud, 1978; Bormann and Gordon, 1984; Sharma and Ambasht, 1986; Rytter, 1989; Elowson and Rytter, 1993; Lõhmus *et al.*, 1996; Son *et al.*, 2007; Tobita *et al.*, 2010).

2.6. Nitrogen fixation in grey alder stands

The species of *Alnus* fix atmospheric nitrogen (N_2) in symbiosis with the filamentous actinomycete *Frankia*. Grey alder is able to cover a large proportion of its annual N demand from atmospheric N (Lõhmus *et al.*, 2002; Mander *et al.*, 2008; **IV**).

N_2 fixing species can increase soil N content. Further, they can significantly affect the soil C pool by increasing detritus inputs or humus formation, or by decreasing the rate of decomposition (Binkley, 2005). Owing to their symbiotic N_2 fixation, alders are known to be beneficial in improving nutrient-poor and degraded soils (Tarrant and Trappe, 1971; Wheeler and Miller, 1990; Bormann *et al.*, 1994; Granhall, 1994; Fisher, 1995; Johnson and Curtis, 2001); they are able to improve soil properties a great deal (Lõhmus *et al.*, 2006), e.g. by phytoremediation of mining areas.

Grey alder stand is a typical ecosystem in the riparian zone. Some studies suggest that alder stands provide very effective protection to waterbodies through effective N and phosphorus removal from the ecosystems

(Mander *et al*., 1995, 1997a, 1997b; Mander *et al*., 2008). However, a few authors have expressed opposite opinions as well (Binkley *et al*., 1992); this inconsistency is mainly due to the different location of the study sites in the landscape.

3. AIMS OF THE STUDY

Since the management of grey alder stands in Estonia is increasing, the need for a more profound knowledge of the functioning of grey alder ecosystems is evident. Further, new silvicultural expertise is needed for environmentally friendly and sustainable managing operations for grey alder stands. Therefore the main aims of the thesis were:

1. to extend the long-term study of the dynamics of the biomass production of grey alder plantation on abandoned agricultural land (**I**, **V**);

2. to estimate grey alder stemwood density (**II**);

3. to estimate the role of the belowground part of grey alder stand on N and C cycling (**I**, **V**);

4. to compile a nitrogen budget of grey alder stand for estimating the rate of annual N_2 symbiotic fixation and to clarify the possible environmental hazards of managing grey alder stands in terms of nitrogen contamination (**IV**).

4. MATERIALS AND METHODS

4.1. Study area (I, II, IV, V)

All data presented in the original research publications included in the current thesis are based on the Holvandi grey alder plantation. The study area is located in South-Eastern Estonia, Põlva county, at 58°3' N and 27°12' E. The mean annual temperature is 6°C, mean precipitation is 653 mm, the length of the mean growing period is 191 days. The meteorological data originates from the Võru meteorological station, which is the closest to the plantation.

The experimental stand was established in spring 1995 on former agricultural land which had been out of use for two years before planting. The planting material was mainly one-year-old and of natural origin. The area of the plantation is 0.08 ha with an initial density of 15,750 ha^{-1}. The soil is classified as Albeluvisol (according to the FAO classification). Neither soil preparation nor any other treatment was done before and after planting. The survival of the plants after the first growing season was very high (Uri and Tullus, 1999).

4.2. Aboveground part of the stand

4.2.1. Estimation of aboveground biomass and leaf parameters (I, V)

Annual measurements (diameter at breast height (DBH); height) of the stand, determining the standing biomass of the plantation, and leaf area index (LAI) measurements were always carried out at the end of the growing period (late August), when the annual production of the aboveground part of the stand had ceased and standing aboveground biomass had reached its maximum.

Dimension analysis (Bormann and Gordon, 1984; **I**) was used for estimation of stand aboveground biomass (AGB). Seven model trees from the middle of the plantation were selected annually for determining the standing biomass and current annual increment (CAI) of the stand. The model trees were selected according to the diameter distribution of the stand. The trees were divided into five diameter classes; from each class one model tree was felled. Additionally, a model tree was felled from classes with a larger number of trees.

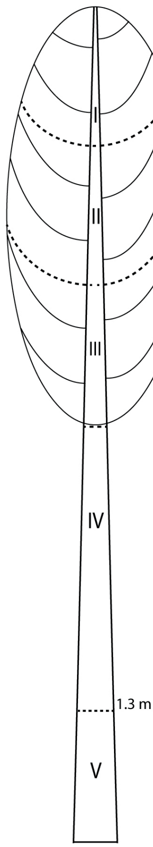

Figure 1. Division principle for the model trees. Roman numerals indicate the sections of the model trees. Dashed lines indicate the borders of the sections.

The model trees were divided into five sections as shown in Figure 1. Stem sections I-III are of equal length. The fresh mass of different fractions (leaves; current year shoots; branches; stem sections) of the model trees were measured *in situ*, subsamples from the each fraction were taken for determining dry matter (DM) and nutrient content. The subsamples were dried at 70°C until constant weight and weighed to 0.01 g. Also the share of the wood and bark of the stems was determined. The dry mass of different fractions was calculated for each model tree by multiplying respective fresh mass by the DM ratio.

The annual production of the stemwood, bark and branches was calculated as the difference between the masses of the respective fractions for the studied year and for the previous year.

The carbon stock in the stems was calculated by using stem mass and C concentration for the fraction.

For estimating leaf parameters, 20-25 leaves from each crown layer of each model tree were randomly collected and oven dried under pressure. Average leaf blade area was measured with the program WINFOLIA (Regent Instruments, INC.); oven dry leaves were weighed to 0.001 g. Thereafter, SLA and LAI were calculated.

To estimate the AGB or LAI of the plantation, an allometric equation (1) provided the best fit:

$$y=aD_{1.3}^{b}, \qquad (1),$$

where, y is the dependent variable (AGB of a model tree (g) or leaf area (m^2)), $D_{1.3}$ is the breast height diameter (cm), *a* and *b* are parameters.

4.2.2. Estimation of wood density (II)

Grey alder stemwood density was estimated in September 2009. Subsamples with a length of 50 cm were taken from the stem sections III, IV and V of the felled model trees. The stem samples were sawn into board in a wood processing laboratory and dried at room temperature. As many branch- and bark-free test pieces (3x2x2 cm) as possible from each test subsample were sawn in accordance with ISO 3131-1975. All test pieces were measured to 0.01 mm and weighed to 0.01 g. All test pieces were dried in the oven at 105°C until absolute dry mass. The volume (2) and density (3) of each absolute dry (moisture content 0%) test piece was calculated as follows:

$$V=abc, \qquad (2),$$

where a, b and c are the dimensions of the test pieces (mm),

$$\varrho=V/m, \qquad (3),$$

where V is the volume of the test pieces (cm^3) and m is the mass of the test pieces (g).

The densities of the test pieces with a moisture content of 12% were calculated as follows:

$$\varrho12=(\varrho w(100+0.6*W))/(0.957(100+W)), \qquad (4),$$

where ϱw is wood density at a room moisture conditions and W is moisture (%) of a room.

4.2.3. Aboveground biomass of understory (V)

For compiling a nitrogen budget of the grey alder stand growing on former agricultural land, the aboveground biomass of the understorey was estimated. Samples were taken at the end of June 2003 when the aboveground biomass of the understorey was at a maximum. The aboveground part of all herbaceous plants was collected from a 1 m^2 quadrate at 10 randomly chosen points over the whole plantation. The samples were dried at 70°C to constant weight and weighed to 0.01 g. As the aboveground part of herbs is annual, its annual production is equal to biomass.

4.2.4. Literature data (III)

The review article (**III)** is based on the data from grey alder yield-tables and other scientific publications. Various yield-tables and data available in the literature were used to describe and compare the growth patterns and production capacity of grey alder mainly in the Nordic and Baltic countries. Yield-tables for grey alder were available from Latvia (Ozols and Hibners, 1927; Murnieks, 1950), Estonia (Raukas, 1930), Finland (Miettinen, 1933), Norway (Børset and Langhammer, 1966), and Lithuania (worked out by Jankauskas) and Belarus (Yurkevich) (Krigul, 1971). As many sources published in the original languages (Latvian, Russian, Estonian) as possible were included in the study in order to summarize the biomass data of grey alder and to extend the knowledge of alder studies conducted in the region. Approximately 70 reported results from differently designed biomass studies from almost 30 literature sources were included in the review (**III**).

4.3. Belowground biomass (I, IV, V)

4.3.1. Coarse roots

Stump and coarse root biomass (CRB) ($d \geq 2$ mm) were estimated by excavation of the root systems of model trees (**I**). The excavation of the root systems of the model trees was carried out in October 1998 and 2003, i.e. for a 5-year-old and for a 10-year-old stand. Minimum, maximum and average stem diameter classes were represented as three model trees were selected randomly according to the DBH distribution. The excavated root systems were washed, placed in plastic bags and separated in the laboratory into the following fractions: roots with diameter d<2; 2≤d<5; 5≤d<10; d≥10 mm and the stump and the nodules. For determination of the DM ratio, a subsample was taken from each fraction; the dried samples were weighed to 0.01 g. The dry mass of each fraction was calculated. The CRB of the stand was calculated by two different methods: (1) use of AGB and the average root ratio (share of the root system in the AGB of the model trees); (2) use of an allometric relationship between DBH and the mass of the root system. Both methods provided similar results for CRB.

The CRB for a 17-year-old stand (**V**) was calculated on the basis of earlier studies (Uri *et al.*, 2009; Lõhmus *et al.*, 1996), where the share of the coarse roots in the aboveground leafless biomass of grey alder stand was approximately 19%. We used the same proportion of coarse roots for calculation of belowground biomass (BGB) from the aboveground leafless biomass. Based on earlier results, we assumed that leafless AGB and CRB develop proportionally. The relative increment of the aboveground part was calculated (production divided by biomass) (5); on the basis of this relative increment the production of BGB was calculated (d>2mm).

$$CRB_{prod}\ (\%) = AGB_{prod} \,/\, AGB \qquad (5).$$

The C stock in the coarse roots was calculated by using CRB and C concentration in the corresponding fraction.

4.3.2. Fine roots and nodules

The soil coring method (Vogt and Persson, 1991) was used for estimating the biomass and necromass of the fine roots (d<2 mm) and nodules in the grey alder stand at the age of 5-**(I)**, 10-**(I)** and 17 years **(V)**. Soil cores were taken randomly over the whole plantation with a cylindrical soil auger in October 1998 (n=20), 2003 (n=25) and 2010 (n=20). The diameter of the cutting edge of the auger was 38 mm. The soil cores reached a depth of 40 cm; they were divided into four equal 10 cm layers. Every single soil core was placed in a polyethylene bag and kept in the refrigerator until further processing. The roots and nodules were washed out of the soil cores during one week after sampling. Further, the fractions of the living and dead fine roots and nodules of alders, as well as the roots of herbaceous plants were separated and cleaned from soil particles under a binocular microscope. The samples were dried up to 70°C and weighed to 0.001 g. The soil core data was used for calculation of the biomass of the fine roots and the nodules per hectare, summing up the average values for the successive soil layers from the soil cores.

The C stock in the fine roots was calculated by using FRB and C concentration in the corresponding fraction.

Fine root efficiency (FRE) was calculated as following: FRE (t t^{-1} y^{-1}) = CAI / FRB

4.3.3. Fine root production

For estimation of annual fine root production (FRP), the ingrowth core method (Ostonen *et al.*, 2005) was used. Altogether 150 ingrowth cores with a diameter of 40 mm and a mesh size of 6 mm were inserted into the soil. The ingrowth cores were inserted in five random transect groups all over the stand, into the topsoil to a depth of 30 cm in October 1999. The ingrowth cores were filled with sieved root-free soil according to the genetic horizons of the soil. A total of 105 ingrowth cores were extracted during 2000-2003: 8 samplings and 15 meshes per sampling. Samplings were carried out in November 2000, in June, August, November 2001-2002 and in June 2003. All obtained subsamples were transported to the laboratory and stored frozen (-18°C) until processing. In the laboratory, the soil cores were divided into depth layers of 0-10, 10-20, and 20-30 cm. The <2 mm roots and nodules were carefully washed out of the soil. The samples were dried up to 70°C and weighed to 0.001 g.

4.3.4. Belowground biomass of the understorey

For compiling the nitrogen budget of the grey alder stand growing on former agricultural land, the BGB of the understorey was estimated on the basis of soil cores (**IV**). Ten soil cores were taken to a depth of 30 cm in the 1 m^2 quadrates using a soil auger (d=108.6 mm). All cores were divided into three subsequent 10 cm layers and the roots and rhizomes were washed out of each layer. The roots and rhizomes of herbaceous plants were separated under a microscope. The samples were dried at 70 °C to constant weight and weighed to 0.001 g.

4.4. Nitrogen budget of grey alder plantation (IV)

Net nitrogen mineralization (NNM) was estimated *in situ* in the upper 10 cm soil layer, using the method of incubated polyethylene bags (Eno, 1960; Adams *et al.*, 1989; Hart *et al.*, 1994; Uri *et al.*, 2003a, 2008). Samples were incubated in April, immediately after the soil had melted; sampling was performed with a monthly interval until the ground was frozen. The N flux from leaf litter decomposition was estimated within NNM. A more detailed description of sampling, sample processing and calculation of NNM and net nitrification is presented in Uri *et al.* (2003a, 2008).

Annual N retranslocation in the alders was estimated using leaf mass and differences in N concentrations between the fresh leaves and leaf litter (Uri *et al.*, 2002). Leaf litter was gathered with 10 litter traps (0.25 m^2 each) during 1998–2004.

N leaching was estimated on the basis of 10 plate lysimeters (stainless steel, collecting area 627 cm^2), which were randomly installed in the soil to a depth of 40 cm in autumn 2002. Water from the lysimeters was sampled monthly from October 2002 to November 2003.

The N_2O flux was measured with the "closed chamber" ("closed soil cover box") method (Denmead and Raupach, 1993; Hutchinson and Livingston, 1993); for determining the N_2 flux, the helium–oxygen (He–O) method (Butterbach-Bahl *et al.*, 1997; Scholefield *et al.*, 1997; Mander *et al.*, 2003; Teiter and Mander, 2005) was applied. Trace gas concentration in collected air was determined using a gas chromatography system (Loftfield *et al.*, 1997). This study was carried out in cooperation with Prof. Ülo Mander's research team from the University of Tartu.

Since the N deposition can be considered a stable parameter for a particular region without big polluters, the value of N deposition reported by Mander *et al.* (1997) was used. The flux of symbiotically fixed N_2 used in the production of alders was estimated by balancing the other fluxes of the N budget (Lõhmus *et al.*, 2002). After estimating the annual N use by plants, leaching and gaseous emission, it was assumed that the budget deficit was covered by symbiotic N fixation.

4.5. Soil sampling and laboratory analysis

Soil was sampled from the studied stand annually during the period of 1995–2008 in October when plant growth had ceased. Ten random points which were evenly distributed over the study area were marked; soil samples were taken adjacent to these points to a depth of 50 cm each year. Soil samples for N were tested according to Kjeldahl. The concentration of organic matter (%) was determined as a loss on ignition at 360°C. Total C concentrations (%) in the soil layers were determined with a CHN analyser (Perkin-Elmer 6400 Series II). For calculation of N and C storage in the soil, soil bulk density from different soil layers (0–50 cm) was determined in 2002. Determination of available phosphorus in the soil was done by flow injection analysis (ammonium lactate extractable). Plant samples were analysed for total N by the Kjeldahl method. Determination of NH_4^+-N, NO_2^--N, and NO_3^--N in the lysimeter water was performed by flow injection analysis. The analyses were carried out at the Biochemistry Laboratory of the Estonian University of Life Sciences.

4.6. Statistical methods and calculations

Normality of variables was checked by the Lilliefors and Shapiro–Wilk tests **(I, II, IV, V)**. The Tukey HSD test in the case of unequal samples sizes **(I, II, V)** and Ficher`s LSD test **(II)** were used for multiple comparison of the means. The t-test was employed to compare means for the two groups **(IV, V).** When data did not follow a normal distribution, or when there occurred inhomogeneity of group variances the non-parametric Kruskal-Wallis analysis of variance was used **(I, IV).** The data of model trees were analysed by correlation analysis (Pearson correlation) **(I, V)** and regression analysis **(I, V)**. Linear and allometric models were employed for estimating relationships **(I, II, V)**. Repeated Measures Analysis of Variance (ANOVA) was used for checking the impact of the stem section on stemwood densities **(II)**. The occurrence of autocorrelation within the FRB data was tested with the Durbin-Watson test (**V**). Fine root mass in the soil cores and SLA were normalized by log- or root transformation **(I)**. Total FRP was calculated on the basis of ingrowth core data and by balancing the biomass compartments of the living and dead roots according to Fairley and Alexander (1985). Fine root turnover rate (y^{-1}) was calculated as annual root production ($g\ m^{-2}\ y^{-1}$) divided by mean FRB ($g\ m^{-2}$) from the ingrowth cores. Fine root efficiency ($t\ t^{-1}\ y^{-1}$) was calculated by dividing stem current annual increment (CAI) by FRB (**V**). Total nitrogen and carbon accumulation in the biomass of fine roots- and nodules was calculated on the basis of average concentration **(V)**. The software STATISTICA 7 (**I, II, IV, V)** and the software SAS 8 **(I)** were used. The significance level $\alpha=0.05$ was accepted in all cases.

5. RESULTS

5.1. Aboveground part of the stand

5.1.1. Dynamics of aboveground biomass (I, V)

Owing to very high planting density, self-thinning of the stand during the first growing decade was particularly intensive. After canopy closure in 1998, the annual mortality of the trees varied between 450 and 2,060 trees ha^{-1} y^{-1}. At the age of 17-years stand density had fallen to 5,100 ha^{-1} (Table 2), i.e. approx. 1/3 of the initially planted trees had survived.

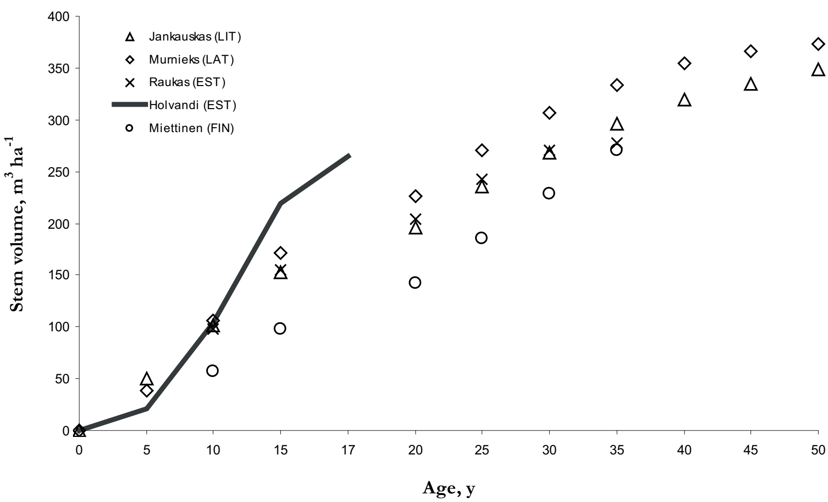

Figure 2. Stem volume dynamics on the basis of yield-tables (Estonia, Finland, Latvia, Lithuania).

Average height and diameter increment was high, exceeding 1 m and 0.5 cm per year, respectively (Table 2), average height and DBH in the 17-year-old stand were 14.3 m and 9.3 cm, respectively.

The increase of AGB has been vigorous (Table 2). In the 17-year-old stand stem mass exceeded 100 t DM ha^{-1} and total woody biomass exceeded 120 t ha^{-1}; C accumulation in stem mass was 52 t ha^{-1}. The CAI achieved a maximum value in the 16-year-old stand, being 14.2 t ha^{-1} y^{-1}. However, in the 17-year-old stand (in 2011) CAI had decreased drastically, being 2.5 times lower than it had been in the previous growth period, most probably due to severe drought. Average stem mass in the 17-year-old stand was 20.7 kg. After converting stem mass into volume units on the basis of stemwood density (subchapter 5.1.2.) the stem volume and CAI of the 16-year-old stand were 251.8 m^3 ha^{-1} and 35.9 m^3 ha^{-1} y^{-1}, respectively. In the 17-year-old stand the respective values were 266.2 m^3 ha^{-1} and 14.4 m^3 ha^{-1} y^{-1}.

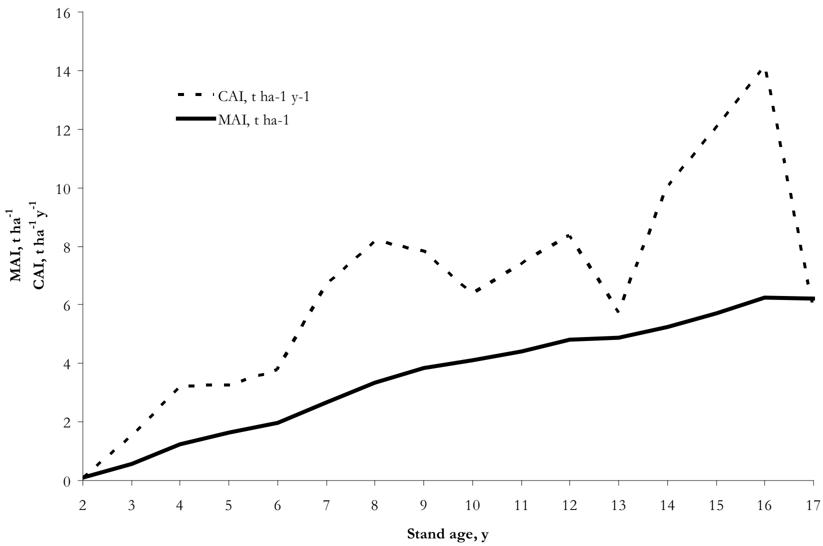

Figure 3. The dynamics of mean annual increment (MAI) and current annual increment (CAI) in Holvandi grey alder plantation.

The annual growth pattern of the grey alder stand was strongly affected by weather conditions. In the droughty summers of 1999 and 2002 the production of both stemwood and foliage biomass was low. Further, a reduction in diameter growth was observed two years following drought (up to 38% lower than before drought). However, stem production decreased in 2002 and even in 2003 but not in 1999 (Table 3 in **I**).

Three different growth functions were tested for predicting an optimal cutting age of the stand on the basis of the data of 12-year time series (**I**). The highest predictions of stem biomass were obtained using the Richards and Hossfeld functions (Table 4 in **I**). The age of maximum mean annual increment (MAI) obtained with the Richards function exceeds 21 years; according to the Weibull function, it is 16 years. The most realistic prediction about stand growth on the basis of predicted stem volume was obtained by using the Weibull function. However, the later actual empirical data did not confirm preliminary prediction since the highest CAI was estimated for the 16-year-old stand (Table 2), instead of the 12-year-old stand.

Table 2. Biomass production and growth dynamics in the Holvandi grey alder stand.

Stand age, y	Biomass, t ha^{-1}	Stem mass, t ha^{-1}	Leaf mass, t ha^{-1}	CAI, t ha^{-1} y^{-1}	MAI, t ha^{-1}	Total production, t ha^{-1} y^{-1}	Stand density, ha^{-1}	$D_{1.3}$, cm	H, m
2	0.4	0.2	0.1	0.1	0.1	0.3	15,750		1.0
3	2.7	1.7	0.5	1.5	0.6	2.5	14,020		2.1
4	7.6	4.9	1.2	3.2	1.2	5.8	13,110	1.9	3.5
5	12.3	8.2	2.0	3.3	1.6	6.7	12,660	2.6	4.6
6	15.9	11.9	1.5	3.8	2.0	6.4	11,910	3.1	5.2
7	25.3	18.6	3.0	6.7	2.7	11.5	9,850	3.9	6.1
8	35.4	26.8	3.2	8.2	3.4	14.0	9,350	4.6	7.2
9	40.4	34.6	1.6	7.8	3.8	9.5	8,400	5.2	8.5
10	49.4	41.0	3.0	6.4	4.1	11.3	7,400	5.7	9.5
12	68.8	57.7	4.0	8.4	4.8	14.0	6,780	6.6	10.8
13	74.3	63.4	4.1	5.7	4.9	12.1	6,175	7.3	11.4
14	87.5	73.5	3.6	10.1	5.3	16.6	5,920	7.8	12.2
15	99.6	85.6	3.4	12.1	5.7	17.2	5,520	8.3	13.0
16	116.9	99.7	3.2	14.2	6.2	22.1	5,360	8.7	13.9
17	120.8	105.4	3.3	5.7	6.2	8.9	5,100	9.3	14.3

5.1.2. Stemwood density (II)

The average stemwood density of grey alder was 396±32 kg m^{-3}. The stemwood density in different stem height sections was significantly different ($P<0.05$): the highest wood density was determined in the highest stem section and the lowest density in the lowermost part of the stem (Table 2 in **II**). There was no correlation between breast height diameter of tree and stemwood density, i.e. the hierarchical position of the tree in the stand did not affect the stemwood density of grey alder.

5.1.3. Foliage characteristics (I)

Average single leaf area of the grey alder model trees in 1997–2005 was 18.6-30.5 cm^2, single leaf mass 0.18-0.27 g and specific leaf area (SLA) 11.6-

13.9 m^2 kg^{-1}. The crown layer displayed significant differences ($P<0.01$) regarding all foliar parameters: the leaves with the largest area and mass were in the highest layer, and both characteristics decreased towards the crown base. The impact of $D_{1.3}$ on single leaf area was insignificant, whereas it was significant on single leaf mass (Gamma correlation, $P<0.01$). The leaves of the trees with a larger diameter had thicker leaves and/or higher tissue density (i.e. lower SLA).

Leaf mass fluctuated around 3 t ha^{-1} since the stand age of 7 years and the LAI values were estimated between 1.38 and 5.43 m^2 m^{-2}. Leaf mass as well as LAI increased with increasing stand age and both stabilized at the stand age of 7 years (Table 2 in **V**). The year affected LAI significantly, being lower in the unfavourable years (Figure 4 in **I**). The LAI and leaf mass were positively correlated ($R^2=0.99$, $P<0.001$).

Leaf N% increased until canopy closure at the stand age of 5 years from 2.77 to 3.94%; after that it stabilized, fluctuating slightly around 3.5%. Foliar assimilation efficiency (FOE) for the same period ranged between 3.4 and 6.6 kg kg^{-1} y^{-1} depending on weather conditions in different years. There was no significant correlation between foliar assimilation efficiency (FOE) and stand age, however, FOE increased in the droughty years when leaf mass and LAI were low (Figure 4, **I**).

5.2. Belowground biomass and production (I, V)

5.2.1. Coarse roots

Total BGB in the 10-year-old grey alder stand was 9.7 t ha^{-1} (CRB 8.7±0.3 t ha^{-1}) (Table 4 in **V**), accounting 16.4% of the total stand biomass (**I**). The estimated CRB in 17-year-old stand exceeded 20 t ha^{-1}. The coarse root annual production was 3.2 t ha^{-1} y^{-1} and 0.7 t ha^{-1} y^{-1} for the 16- and 17-year-old stand, respectively (Table 4 in **V**). The mean annual coarse root production for 17-year old stand was 1.2 t ha^{-1} y^{-1}. The C stock in CRB in 17-year-old stand was 11 t ha^{-1}.

5.2.2. Fine roots and nodules

Total standing FRB has been low throughout the study period, being less than 1 t ha^{-1}. The FRB in grey alder stand stabilized already at the stand age of 10-years; in 17-year-old stand it was almost the same (Table 3). Main share of the FRB (47-57%) was always located in the upper 0-10 cm soil layer and in deeper soil layers has not changed significantly throughout the studied period (Figure 4). However, the FRB per tree had increased continuously throughout the stand development. Fine root necromass in soil was very low (10-20 g m^{-2}) (Table 3). The C accumulation in fine roots has been low (<0.5 t ha^{-1}). The nodule biomass (NB) in 17-year-old stand was 31±19 g m^{-2}; it was accumulated mostly evenly in the upper 20 cm soil layer (Figure 3 in **V**). The NB increased during stand development but in the same time the number of nodules decreased. The vertical distribution of the nodules has changed to more even in 17-year-old stand compared to the earlier stages (Figure 3, **V**).

Table 3. The dynamics of fine root and nodule biomass and necromass (mean±standard error) in the grey alder stand growing on abandoned agricultural land.

Stand age, y	Coarse root biomass, t ha^{-1}	C accumulation in coarse roots, t ha^{-1}	Coarse root production, % of biomass* / t ha^{-1}*	Fine root biomass, g m^{-2}	C accumulation in fine roots, t ha^{-1}	Fine root necromass, g m^{-2}	Nodule biomass, g m^{-2}	Nodule necromass, g m^{-2}
5	2.0	1.0	37.9 / 0.76	55±11	0.28	-	17±8	-
10	8.7	4.3	16.4 / 1.43	87±14	0.44	19±4	16±6	2±1
17	22.3*	11.0	3.3 / 0.33	81±10	0.41	11±2	31±19	1±1

* – Calculated

The FRB in the ingrowth cores was low during the first two growing seasons (2000 and 2001) after incubation. After one growing season, in November 2000, FRB was 15 g m^{-2} in the 0-30 cm topsoil and 50% of FRB was located in the upper 10 cm soil layer. The highest standing FRB for the 0-30 cm soil layer was obtained in the third growing season (June 2002), reaching 123 g m^{-2} (Figure 2 in **V**).

Fine root net primary production (NPP) was the highest in the upper 10 cm soil layer. The estimated annual fine root NPP in the 9-year-old stand was 53 g m^{-2} y^{-1}; the turnover rate of the fine roots was 0.54 and longevity 1.9 y. The NPP values for the 5- and 17-year-old stands, calculated on the basis of fine root biomass and turnover rate were 30 and 44 g m^{-2} y^{-1}, respectively.

A strong positive correlation was found between FRB per tree and stand age (Figure 4 in **V**); an analogous relationship was established between FRB and stand's basal area or stem mass (Figure 5 in **V**). The fine root efficiency (FRE) was the highest at the stand age of 10 years (7.3 t t^{-1} y^{-1}).

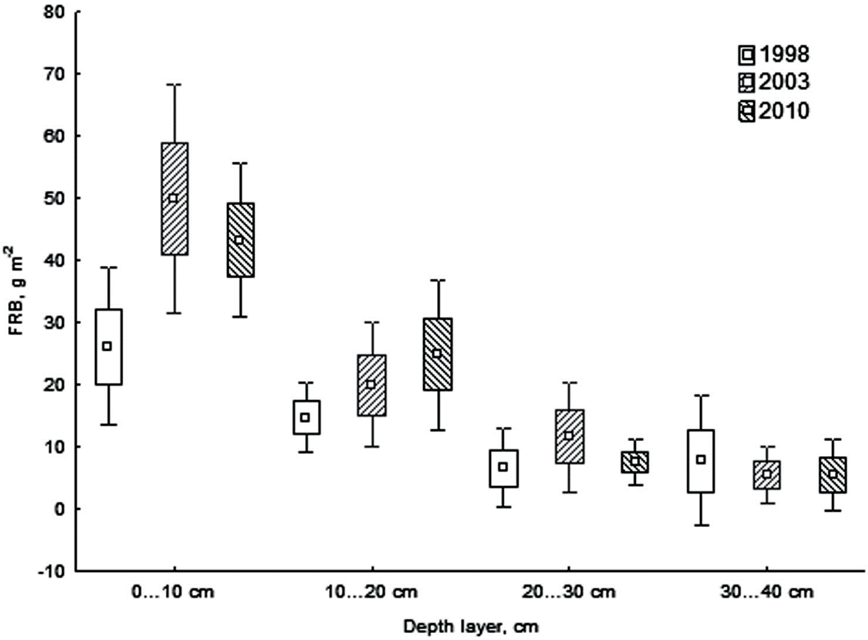

Figure 4. The vertical distribution of fine roots in the grey alder stand at the ages 5, 10 and 17 years. Boxes indicate mean ± standard error; whiskers indicate the 95% confidence intervals.

5.3. Nitrogen fluxes (IV)

Annual net nitrogen mineralization (NNM) in the 0-10 cm soil layer was 74 kg ha^{-1} y^{-1}. Annual N input in the soil via leaf litter was 95.4 kg ha^{-1} y^{-1}. Weather conditions influenced significantly N retranslocation from senescing leaves, being in the range of 3-10% as it was significantly higher (>20%) in the droughty years of 1999 and 2002. The total annual leaching of different forms of N was estimated at 14.9 kg ha^{-1} y^{-1}. The main forms of leached N were organic N (51.6%) and nitrate (48.2%). Maximum leaching occurred in September. The average N_2O-N and N_2-N fluxes were 0.14±0.12 mg N_2O–N m^{-2} d^{-1} and 20.2±12.2 mg N_2–N m^{-2} d^{-1}. Thus, the annual flux of N_2O-N and N_2-N, was 0.50±0.45 and 74±45 kg N ha^{-1} y^{-1}, respectively.

5.4. Nitrogen budget and symbiotic nitrogen fixation of the grey alder plantation (IV)

The amount of N used for the annual production of tree biomass in the aboveground part of the 10-year-old grey alder stand was 149 kg ha^{-1} y^{-1}; 70% of this was accumulated in the leaves and 17% in the stemwood (Table 2 in **IV**). Total N accumulation in the aboveground biomass of the 10-year-old trees amounted to 301 kg ha^{-1}.

Nitrogen use efficiency (NUE) during the study years (stand age 2-10) was stable (Figure 1 in **IV**), a significant increase in NUE was noted in 2002 (drought).

Symbiotic nitrogen fixation was 151.5 kg ha^{-1} y^{-1}, which covered 74% of the annual N demand of the plants (Table 2 in **IV**). Symbiotic fixation per 1 kg of nodule mass was 0.97 kg N y^{-1}.

Annual symbiotic nitrogen fixation in the 10-year-old grey alder stand growing on abandoned agricultural land covered an essential part of the plants' annual N demand. However, possible environmental risks as leaching (14.9 kg ha^{-1} y^{-1}) or N_2O emission (0.5 kg ha^{-1} y^{-1}) were small. Probably, the bulk of leached N was accumulated in the 40-50 cm soil layer where the N pool increased significantly during the first 14-years of stand growth (Figure 2 in **IV**).

5.5. Soil (IV, V)

Grey alder stand affects significantly N cycling and the soil N and C status. At the establishment of the plantation (1995) the total N pool in the upper 20 cm layer was 2.70 t ha^{-1} while 1.39 t ha^{-1} was accumulated in the 0-10 cm soil layer. During 16 growing years (1995–2010) a significant flux of N reached the soil with leaf litter. The N pool in the 0-10 cm soil layer in the 17-year-old stand had increased to 2.06 t ha^{-1} (Figure 5). The increase in soil N during 14 years was statistically significant in the 0-10 cm ($R=0.88$; $P<0.01$) and 40-50 cm ($R=0.67$; $P<0.05$) soil layers (Figure 2 in **IV**).

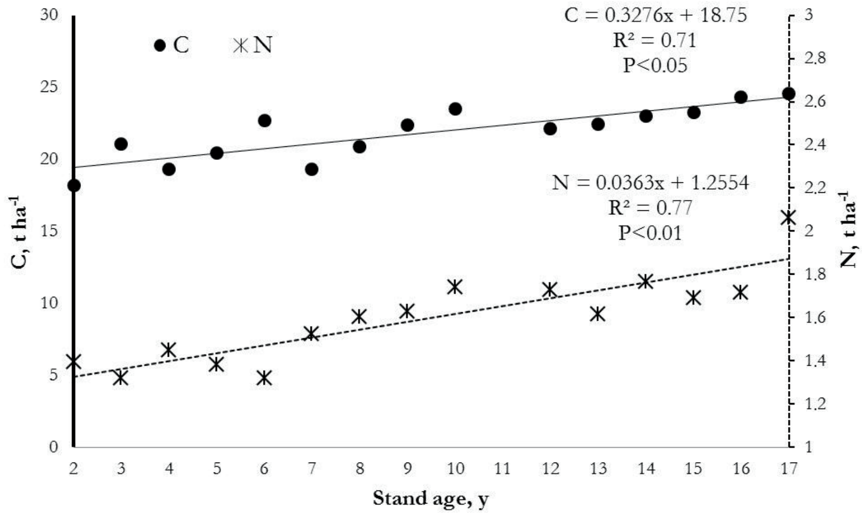

Figure 5. Carbon (C) and nitrogen (N) dynamics in the upper 10 cm soil layer of the grey alder stand growing on former arable land.

Acidification of the soil was significant; the soil pH value decreased by 1.3 units during the first 14-years of stand growth (Figure 6). However, the pH decrease was the most drastic during the first decade after the establishment of the stand; later soil pH stabilized.

At the establishment of the plantation the C pool in upper 0-10 cm soil layer was 18.2 t ha^{-1}; in the 17-year-old stand it was 24.5 t ha^{-1}. More than 6.0 t C ha^{-1} was accumulated in the soil during the 17-year period (Figure 5). Since the content of organic carbon in the upper 0-10 cm soil layer increased significantly, the soil of a grey alder stand on abandoned agricultural land acts as a carbon sink.

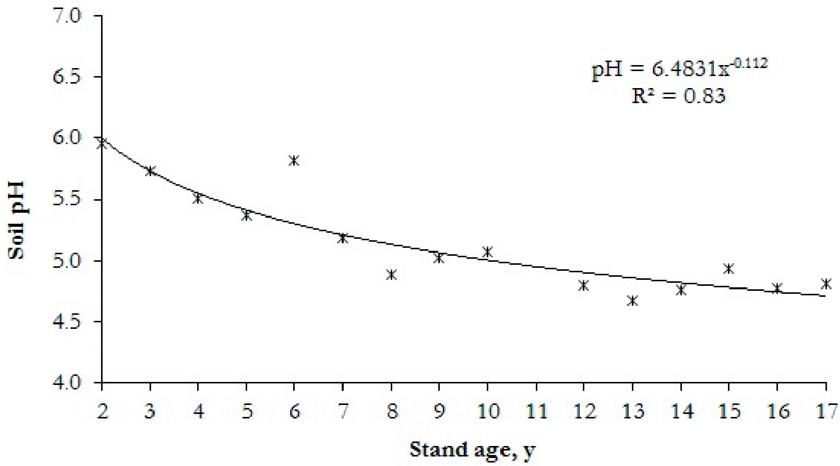

Figure 6. The dynamics of soil pH in the upper 10 cm soil layer of the grey alder stand growing on former arable land.

6. DISCUSSION

6.1. Dynamics of aboveground biomass

Grey alder is well known as a highly productive tree species in forests of the Nordic and Baltic countries both on mineral and organic soils (Granhall and Verwjist, 1994; Saarsalmi, 1995; Rytter, 1996; Telenius 1999). Our study has confirmed this standpoint. However, cultivation of grey alder stands is very rare in Estonian forestry due to the low economic value of grey alder timber. New data, provided in the present study, improve the knowledge of the production potential of this species, perspective as a bioenergy source.

The height and diameter growth and the volume increment of the stand as well as the self-thinning process of the grey alder plantation on former agricultural land were intensive (Table 2; Figure 1 in **I**).

In the 17-year-old stand the stem volume was 266 m^3 ha^{-1} which exceeds the highest corresponding values of all grey alder yield-tables analysed in paper **III** where the highest stand volumes at the age of 15 and 20 years were 170 m^3 ha^{-1} (Latvia) and 225 m^3 ha^{-1} (Latvia, Norway), respectively (Figure 2; Figure 2 in **III**). Further, at the age of 17 years the stem volume of the studied stand exceeded the corresponding values of stands of similar age reported in the literature (Utkin *et al.*, 1980; Johansson, 2000; Hytönen and Saarsalmi, 2009).

The current annual increment (CAI) of stem mass fluctuated, depending strongly on the weather conditions during the growing period as well as on stand age. In the 16-year-old stand CAI was as high as 36 m^3 ha^{-1} y^{-1}, which is a remarkable value for Estonian conditions. The annual biomass production of all aboveground fractions – the stem, the branches and the leaves – was negatively affected by the droughty growing period. A decrease in the production of the leaves and the branches occurred in the very dry years of 1999 and 2002. However, stem production decreased in 2002 and even in 2003 but not in 1999 (Uri *et al.*, 2002).

As the purpose of SRF stand is to obtain the highest bioproduction in the shortest time period possible, the age of bulk maturity indicates the length of the rotation period of the stand. The first CAI peak occurred at the stand age of 12 years after which it started to decrease. Assuming that this trend exists, a model was developed and the bulk maturity of the stand was predicted to occure at the age of 16 years (**I**). However, after a temporary decrease the growth of the stand accelerated peaking in the 16-year-old stand when CAI reached as high as 36 m^3 ha y^{-1}, which was the maximum estimated CAI value during the 17-year study period. Regarding such a growth pattern, the bulk maturity of the stand is reached later. According to our latest measurement data for the 17-year-old stand, CAI was 2.5 times lower, which is most probably caused by the interaction between the droughty growth period and the forthcoming bulk maturity of the stand which occurred later than predicted in paper **I**.

Hence, at the approximate age of 20 years the grey alder stand has probably reached the earliest cutting age for SRF in Estonian conditions. This finding is in good accordance with the data of several earlier studies (Rytter, 1995; Lõhmus *et al.*, 1996; Rytter *et al.*, 2000; Daugavietis *et al.*, 2009; **I**) as well as with the data of the yield-tables reported in paper **III** where the rotation length of 15-20 years is recommended. High production and growing stock values indicate the great potential of grey alder for SRF species.

Another important issue related to SRF stands is initial stand density. The economic efficiency of SRF depends on the establishment costs of plantation. Thus optimal initial density is crucial in the economic aspect of SRF, affecting the cost of the initial establishment- and also the further management of the stand. In the Holvandi plantation, initial density was very high (15,750 ha^{-1}), which is inherent for naturally regenerated grey alder stands. In several grey alder experimental plantations, applied high initial density ranged between 15,000 ha^{-1} to 40,000 ha^{-1} (Saarsalmi *et al.*, 1985; Hytönen *et al.*, 1995; Rytter, 1995; Hytönen and Saarsalmi, 2009). However, as high initial density is accompanied by the rapid decrease in number of trees (Figure 3 in **III**) it can be considered unreasonable for the plantation considering its high establishment costs. Suggestions about density and thinnings in alder stands are conflicting. According to an experiment by Rytter (1995), thinnings may not benefit higher bioproductivity of the alder stand; the same amount of biomass was produced both in a thinned and in an unthinned stand. However, according to the yield-tables presented in paper **III**, densities at the age of 15-20 years in the most productive stands range between 2,400 ha^{-1} and 8,000 ha^{-1}. Also Miežite (2008) suggests a density of 3000 ha^{-1} for a biomass production-oriented grey alder stand at the age of 14-17-years. Optimal initial stand density can be derived from the number of trees at the age of stand harvest. Thus, it seems that initial density over 10,000 ha^{-1} is not justified and optimum final density for the grey alder plantation should range between 3,000-6,000 ha^{-1}. In the Holvandi stand density at the age of 17 years was 5,100 ha^{-1}; any silvicultural treatments were applied throughout the growth of the stand. Hence, the density of an almost matured stand can be considered as an optimum. Moreover, this is consistent with the stand density values of the most productive yield-tables, reported in paper **III,** where they ranged from 2,700 ha^{-1} to 6,500 ha^{-1}at the age of 15 years. Hence, it can be supposed that a lower initial plantation density would also ensure high biomass production.

As the exploitation of grey alder wood most probably increases in the nearest future, the need for more adequate grey alder stemwood density estimation is evident. In the present study it was necessary to estimate exact stemwood density for converting biomass units to volume units, commonly used in practical forestry. Exact stemwood density values allowed to reliably compare the dynamics of the Holvandi stand's growth with the relevant data of the yield-tables (**III**). The use of stemwood density data from other countries is quite limited due to their high variability. Wiemann and Williamson (2002) reported that the mean wood specific gravity of angiosperms gradually increases with decreasing latitude. In Table 3 in paper **II** the data of grey alder wood densities from different countries support this theory as the wood density values from the northern latitudes are much lower than those from the southern latitudes.

6.2. Dynamics of belowground biomass

Paper **IV** presents the results of the fine root and nodule dynamics of the Holvandi grey alder plantation during the 17-year time-series period. Generally, data about nutrient accumulation and biomass of the belowground part of alder stands are scarce in the literature, with only a few available sources (Bormann and Gordon, 1984; Rytter, 1989). Relevant data about the FRP of grey alders are lacking despite the evident importance of this flux in N or C budgeting. In the present study the optimum supply of fine roots for functioning of the stand was established already at the age of 10 years and it was similar for the 17-year-old stand (<1 t ha^{-1}). The main part of fine roots was allocated in 0-10 cm topsoil. Such FRB can be considered low for boreal and temperate forests. Due to low FRB, the amount of C accumulated in the fine roots is also low (<0.5 t ha^{-1}), and thus the role of fine roots in the C stock of stand is modest.

An average FRB value of 230 g m^{-2} for boreal forests was reported by Jackson *et al.* (1997). However, according to a study of Finer *et al.* (2011), average FRB in boreal forest is higher, ranging from 526±321 g m^{-2} up to 775±474 g m^{-2} in temperate forest.

The low FRB of the stand is in good accordance with literature data: Bloom *et al.* (1985) claimed that trees growing at infertile sites should allocate a greater proportion of their resources into FRP than those growing at fertile sites. In the soil of the plantation, N content in the topsoil was high. According to literature data, nitrogen limitation in the soil increased the FRB of different tree species (Finer *et al.*, 2007; Helmisaari *et al.*, 2007; Graefe *et al.*, 2010). Compared to initial soil N content it increased significantly in the 10- and 17-year-old stands (**V**).

In the ingrowth cores FRP was very low in the first and the second growing year (**V**). This is in good accordance with earlier studies (Vogt *et al.*, 1998; Makkonen and Helmisaari, 1999; Ostonen *et al.*, 2005). It was shown that the disturbance causeb by installation of cores, inhibited root growth into ingrowth cores during the first two years. FRP in the studied plantation was low (54 g m^{-2}), which may have been caused by the droughty summer (Nikolova *et al.*, 2009). On the other hand, low FRB and FRP indicate high fine root efficiency (FRE), which is described as an intensive fine root strategy (Lõhmus *et al.*, 2006; Ostonen *et al.*, 2011). In fertile soils high fine root biomass is not necessary for a tree to grow a large amount of fine roots for maintaining itself. In the case of an intensive strategy, trees increase the efficiency of fine roots and rhizosphere processes (Leuschner *et al.*, 2004; Lõhmus *et al.*, 2006; Ostonen *et al.*, 2011). Trees using an extensive strategy increase the mass, surface area and length of fine roots. In the studied stand the difference between the soil-root interface and bulk soil microbial activity and diversity was markedly higher than in grey alder stands growing on forest land (Lõhmus *et al.*, 2006). A possible explanation for this is that more assimilates are located belowground to support rhizosphere processes for effective nutrition. In the Holvandi stand also specific root area (SRA; m^2 kg^{-1}) was significantly higher (Lõhmus *et al.*, 2006) than in natural alder stands, and it showed positive correlation with activity of microbial communities. Hence both low fine root biomass and turnover rate indicate the significantly greater role of the intensive fine root strategy in the studied grey alder stand. However, in some forest ecosystems the production of the belowground part of stand may account for up to 75% of total annual production (Jackson *et al.*, 1997).

The FRE was the highest at the age of 9-10 years of the stand, – i.e. in the droughty years of 2002 and also in 2003. Apparently, it is more economical for a tree to adapt the functioning of its fine root system to the unfavourable conditions rather than to grow a large amount of new roots for supply its needs. Further, at the stand age of 9-10 years, due to high stand density, light competition between the trees was severe. Hence, for surviving in such conditions, it was more important and profitable for a tree to enlarge its aboveground part and to operate its root system very efficiently. At the age of 17 years stand density and the increment of stem mass had declined compared to the 10-year-old stand; also FRE had slightly decreased.

An essential flux of nutrients and carbon reaches the forest soil through root litter. Dead fine roots of grey alder should decompose fast in favourable conditions. The rate of decomposition depends on soil temperature and soil water availability (Santantonio and Hermann, 1985). Furthermore, the high content of N in fine roots (1.25%) and a favourable C/N ratio promote the decomposing of fine roots, which is therefore rapid. Hence, the necromass of fine roots in the plantation soil remains low.

As alders are N_2 fixing tree species, it is essential to estimate the biomass of nodules. This parameter varies depending on tree size, stand density (Bormann and Gordon, 1984) and stand age (Sharma and Ambasht, 1986; Son *et al.*, 2007). In the 17-year-old stand the NB value, compared to that of the 10-year-old stand, had doubled, reaching up to 30 g m^{-2}. NB in a 4-year-old grey alder coppiced stand in Finland was found to be 25–29 g m^{-2} (Saarsalmi *et al.,* 1985); Bormann and Gordon (1984) found that the average mass of the nodules in a 5-year-old *Alnus rubra* stand was 15 g m^{-2}. With increasing stand age, as trees grow larger, the mean weight of nodules increases and the number of nodules decreases (Tobita *et al.*, 2010). According to Bond *et al.* (1954), increasing soil N content increases nodule weight. In our study soil N content in the plantation increased significantly during stand growth (Table 1 in **IV**).

6.3. The effect of growing grey alder on the soil nitrogen and carbon status

The initial soil N pool in the upper 0-20 cm layer (2.70 t ha^{-1}) of the stand fits the range of the overall N pool in boreal forest ecosystems, which varies 1-8 t ha^{-1} (Gundersen, 1995). According to Kask (1975), the average nitrogen storage in Estonian agricultural soils ranges between 3 and 9 t ha^{-1}.

The effect of alders on the content of soil N and C was significant and fast. Both N and C content in the upper soil layer in the grey alder stand increased significantly during the study period (Table 1 in **IV**).

The average annual increase of the N pool in the 0-10 cm soil layer during 14 years was 26.4 kg N ha^{-1} y^{-1}. After the first five years the increase in soil Kjeldahl nitrogen was statistically insignificant ($P>0.05$) due to the small dimensions of the trees and the modest N flux into soil via leaf and root litter. The effect of alders on enrichment of the soil with N was revealed after the sixth growing year ($P<0.05$). Later on the N input increased and in the 17-year-old stand soil N content had increased notably (Figure 5).

The literature presents a few results about annual N accumulation in alder stands (DeBell and Radwan, 1979; Binkley, 2005); the reported values vary to a large extent. Compared to the riparian grey alder stand (Mander *et al.*, 2008), the value obtained in this study was 3.5 times lower, but compared to a degraded soil at higher latitudes (Myrold and Huss-Danell, 2003), our value was 3-9 times higher. Hence, N accumulation is strongly dependent on stand age and on the impact of environmental factors and site quality. In forest ecosystems FRB is an important factor affecting N and C accumulation in the soil. However, only 3.4% of the total N pool and 0.6% of the total C pool in the tree biomass of the 17-year-old grey alder stand is accumulated in fine roots. Thus, the main input of N and C into soil in grey alder stand orginates from leaf litter. N_2 fixing trees are able to significantly affect the soil C pool by increasing detritus inputs or humus formation, or by decreasing the rate of decomposition (Binkley, 2005). The total C stock in the soil of the studied stand increased significantly, which is in accordance with other studies carried out in SRF stands (Liski *et al.*, 2001).

Annual N and C inputs into the soil via leaf litter are mainly dependent on the current year mass of the foliage. Annual foliage production and mass were around 3-4 t ha y^{-1} after the stand age of 7 years. However, weather conditions affect leaf production markedly, being lower in droughty years (Figure 1 in **V**) and, hence also the N input into the soil was lower. Consequently, the N flux introduced into the soil via leaves depends significantly on growth conditions, stand age, etc.; therefore the values presented in the literature vary a great deal, from 12 to 300 kg ha^{-1} y^{-1} (Tarrant and Trappe, 1971; Turner *et al.*, 1976; Binkley, 1981; Rytter, 1989). Grey alder affects, besides soil nutrient content, also soil pH as well. Soil pH decreased significantly in the upper 0-10 cm soil layer – 1.3 units during 14-years of observation. No significant pH decrease was observed in the deeper soil layers (10-40 cm). However, in the 40-50 cm soil layer where the acidifying effect was detected, pH decreased 1.0 units.

Most likely pH decreased both due to symbiotic nitrogen fixation and high nitrification rate. The acidifying effect of alder stands is stronger at the very beginning of stand development. In Holvandi, acidification declined after canopy closure, at the stand age of 7 years. A similar trend is reported by Lõhmus *et al.* (2006) for a common alder stand growing in an afforested mining area. Studies by Van Miegroet and Cole (1985) and Cole *et al.* (1991) reveal similar effects in red alder stands as in droughty years, due to shortage of water (in the studied stand in 1999 and 2002), NNM and nitrification decreased while soil pH increased.

Increased soil acidity may reduce the production of the next forest generation. Therefore, after cutting alder stand, the area should be cultivated with some non-leguminous species. Gundersen *et al.* (2006) suggest liming for lowering soil acidity.

6.4. Nitrogen budget of grey alder stand

With the increasing stand age the N demand of the stand decreased mainly because of the lower understorey biomass in the 10-year-old stand compared to the 5-year-old stand. After canopy closure a significant decrease of understorey biomass occurred, which led to a reduction in annual N use. The N demand of the trees rose due to the increased wood production. According to many studies, the CAI of grey alder stand peaks at the age of 15-20 years. The N demand of the trees peaks at the same age after which it should remain stable or start to decrease.

Higher N demand at younger stand age was also reported for a grey alder riparian stand (Mander *et al.*, 2008). However, the N demand of the foliage remained stable as leaf biomass stabilized around 3 t ha^{-1} at the stand age of 7 years (**I**). In the 10-year-old stand total N bound in woody biomass amounted to ~200 kg ha^{-1}. Hence, in the case of full tree harvesting N loss from the site would be modest compared to the total stand N pool in the plants (~350 kg ha^{-1}) or in the soil (~3 t ha^{-1}).

The N retranslocation from the senescent leaves is an essential adaptation of trees for efficient nutrient use, but for N_2 fixing tree species like alders modest annual N retranslocation is inherent. Furthermore, also the retranslocation flux is affected by the year, being higher in droughty years. After excluding the droughty years from analysis average retranslocation in the Holvandi plantation was 3-11% of total foliage N while in the droughty years (1999 and 2002) it was significantly higher, 23% and 20% of the total leaf N pool, respectively (**IV**). Similar values (8-14%) are presented by Mander *et al.* (1997) as estimated for natural grey alder stands.

Alders cover a large part of their annual N demand via symbiotic N_2 fixation. The ability to fix N_2 depends on many factors: soil properties (Johnsrud, 1978); NB and alder species (Binkley, 1981; Rytter, 1989); stand density (Bormann and Gordon, 1984); stand age (Lõhmus *et al.*, 2002). Literature data about N_2 fixation from different stands is very variable, ranging in the interval of 28-185 kg N ha^{-1} y^{-1} (Johnsrud, 1978; Tripp *et al.*, 1979; Lõhmus *et al.*, 2002). In the Holvandi study area symbiotic nitrogen fixation covered 74% of the total annual stand N demand (151.5 kg ha^{-1} y^{-1}), which is an average result compared to other literature data.

The N content in leaf litter is high, reaching 20-40 g kg^{-1} (Rytter, 1990; Saarsalmi, 1995; Uri *et al.*, 2003b); due to the favourable C/N ratio the decomposition of leaf litter is fast. The annual NNM flux in the 0-20 cm soil layer of the Holvandi grey alder plantation was stable in the 5- and 10–year-old stand, 141 kg ha^{-1} y^{-1} and 124 kg^{-1} ha^{-1}, respectively. In the 10-year-old stand annual NNM covered 60% of the demand of the stand vegetation.

The N leaching was at its maximum in September when N uptake by the plants had ceased. At the same time, leaching was promoted by the intensive decomposition of leaves and understorey plants. However, the percentage of the leaching flux in the total N budget was quite modest (~15 kg ha^{-1} y^{-1}). According to Binkley *et al.* (1992), N leaching may amount to 5-50 kg ha^{-1} y^{-1} in red alder-conifer mixed stand. There are various opinions about the N pollution hazard to groundwater after clear-cutting (Van Miegroet *et al.*, 1992). An N leaching of 9-13 kg ha^{-1} y^{-1} was measured in grey alder stands of riparian buffer zones (Mander *et al.*, 1997). However, a study based on the clear-cut area in a 32-year-old grey alder stand on forest land showed that the new generation of the alder root suckers and the lush vegetation eliminate the hazard by using soil N (Becker, 2012).

Gaseous N loss in the studied grey alder stand was notable; gaseous N emitted mainly in the form of N_2 (73.8 kg N ha^{-1} y^{-1}). The flux of N_2O from the Holvandi plantation was negligible (0.14 kg N_2O-N ha^{-1} y^{-1}) but it is comparable with the corresponding data reported by Teiter and Mander (2005) and Mander *et al.* (2008) – 0.2-0.7 kg N_2O-N ha^{-1} y^{-1}.

7. CONCLUSIONS

The first hypothesis was verified: the biomass production of the studied grey alder stand growing on abandoned agricultural land was very high (**I**, **V**); exceeding the corresponding values of several yield-tables (**III**). Grey alder can be considered a suitable tree species for SRF and it can be a promising source of bioenergy in Estonia and also in neighbouring region. Several studies on the productivity, growth and yield of grey alder proved its high productivity both on mineral soil and on peatland. According to the yield-tables analyzed in paper **III**, the Baltic countries are the most favourable region for growing grey alder.

The optimal initial density of biomass production-oriented grey alder plantation, to ensure high productivity, is in the range of 3,000 ha^{-1}-6,000 ha^{-1}. The optimal rotation period for grey alder SRF stand is between 15-20 years (**III**, **V**). The estimated growing stocks according to the yield-tables analyzed range from 140 m^3 ha^{-1} to 225 m^3 ha^{-1} at the age of 20 years. In the studied stand stem volume and stand density at the age of 17 years were 265 m^3 ha^{-1} and 5,100 ha^{-1}, respectively (**V**).

The CAI of grey alder stand is very fluctuating, depending significantly also on weather conditions in the growing period and on stand age (**I**, **V**). The maximum CAI value of the studied stand was 36 m^3 ha^{-1} y^{-1} at the age of 16 years. According to an assumption made on the basis of CAI and MAI, optimal rotation length for grey alder stand as SRF management is approximately 20 years.

Average stemwood density in the studied stand was 396 kg m^{-3}, which is in good accordance with earlier studies; it increased gradually from the stump towards the crown. No correlation was found between breast height diameter of tree and stemwood density (**II**).

The second hypothesis was not verified. The FRB and NB of the grey alder plantation on fertile soil were low (**I**, **V**); it had reached its maximum already at the age of 10 years. Since FRP was modest, the N or C flux into the soil via root litter was small. Due to favourable soil conditions the decomposition of dead fine roots was extremely rapid and the necromass of fine roots was very low. The fine root annual production of the stand was modest, fine root turnover rate was 0.54 and average longevity of fine roots was 1.9 y. A strong positive correlation was established between FRB and stand basal area.

Annual symbiotic nitrogen fixation in the 10-year-old grey alder stand growing on abandoned agricultural land was 150 kg ha y^{-1}; it covered an essential part of the plants' annual N demand (**IV**).

The third hypothesis was also verified: grey alder stand affects significantly the soil N and C status. The soil N and C storage in the upper 10 cm layer in the 17-year-old stand was 670 kg ha^{-1} and 6.3 t ha^{-1} larger from the initial storage, respectively (**IV**, **V**). Both the N and C fluxes into the soil were strongly contributed by leaf litter as the annual fine root production was low. Grey alder stand on abandoned agricultural land acts as an effective C sink both for soil and tree biomass.

Soil acidification was noted during stand development. However, it can be easily mitigated by liming or by using silvicultural treatments.

The fourth hypothesis was verified as well: the environmental risks (N leaching; N_2O emission) were negligible (15 kg ha^{-1} y^{-1} and 0.5 kg ha^{-1} y^{-1}, respectively). The leached N was accumulated in the deeper 40-50 cm soil layer and gaseous N emission was mainly emitted in the form of harmless N_2 (**IV**). Hence, we can conclude that grey alder is a potential resource of bioenergy. Large scale establishment of alder stands on abandoned fields does not involve considerable environmental risks.

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SUMMARY IN ESTONIAN

Viimasel poolsajandil on Eestis hall-lepikute pindala ja tagavara märgatavalt kasvanud (Aastaraamat Mets 2010), seda enamasti endiste põllumaade arvelt. Peale taasiseseisvumist jäi Eestis kasutusest välja hinnanguliselt 300 000–400 000 hektarit põllumajanduslikke maid, mis osaliselt metsastusid. Tänu heale levimisvõimele, kiirele kasvule, vitaalsusele noores eas ning heale kohanemisvõimele on hall lepp olnud üheks peamiseks põllumaid asustavaks pioneerpuuliigiks. Statistilise metsainventuuri (SMI) järgi on praegu Eesti hall-lepikute pindala ligikaudu 187 000 hektarit ning puistute tagavara 31 miljonit m^3, mis moodustab 6,7% meie metsade kogutagavarast (Aastaraamat Mets 2010). Halli leppa leidub arvestataval määral ka meie naaberriikides – Lätis on hinnatud lepikute tagavaraks 31 miljonit m^3 (Miežite, 2008), Leedus 21 miljonit m^3 (Forest statistics Lithuania 2009), Rootsis 49 miljonit m^3 (Swedish statistical yearbook of forestry 2009).

Fossiilkütuste viimaste aastate kõrged hinnad ning Euroopa Liidu kliimapoliitilised eesmärgid on sundinud riike üha enam panustama taastuvenergiale ning otsima alternatiivseid taastuvaid energiaallikaid. Tänu Läänemere regiooni suurele metsasusele on selles piirkonnas üheks taastuvenergiaallikaks puit. Hall lepp on üks kiiremakasvulisi puuliike Põhjamaades ning Baltikumis – ta on näidanud head produktsioonivõimet nii turvas- kui ka mineraalmuldadel (Granhall ja Verwjist, 1994; Saarsalmi, 1995; Rytter, 1996; Telenius, 1999) –, ja on perspektiivne energiametsanduse puuliik. Sugugi vähetähtis pole ka asjaolu, et sümbiontselt lämmastikku siduva liigina parandab hall lepp suurel määral kasvukoha mullaomadusi.

Käesolevas töö raames hinnati endisele põllumaale rajatud hall-lepiku bioproduktsiooni, lämmastikuringet, süsiniku sidumise võimet ning hall-lepikute majandamisega kaasneda võivaid võimalikke keskkonnamõjusid. Töö põhineb endisele põllumaale rajatud halli lepa katsekultuuris läbi viidud pikaajalisel uuringul.

Käsitletakse järgnevaid teemasid:

- halli lepa maapealne biomass ning leheparameetrite dünaamika (**I, V**);
- puistu maa-alune biomass ja produktsioon (**I, V**);
- halli lepa tüvepuidu tihedus (**II**);

- lämmastikuringe peamised vood ning varud endise põllumaa hall-lepikus (**IV**);
- süsiniku akumulatsioon puistu biomassi ja mulda (**V**);
- halli lepa bioproduktsioon ning majandamine Põhjamaades ja Baltikumis; ülevaade kirjanduse põhjal (**III**).

Töös püstitati järgmised hüpoteesid:

1. Endisel põllumaal kasvav hall-lepik on kõrgproduktiivne. Lühikese raieringiga majandatava hall-lepiku mahuküpsus saabub 15–20 aasta vanuses, mis on biomassi tootmise eesmärgil kasvatatava puistu puhul optimaalne raieringi pikkus.

2. Peenjuured etendavad tähtsat rolli puistu lämmastiku ning süsiniku sidumises.

3. Noor halli lepa puistu toimib süsiniku sidujana ning puistu positiivne mõju mullaviljakusele avaldub juba noores eas.

4. Hall-lepiku kasvatamisega endisel põllumaal ei kaasne märgatavaid keskkonnariske (N_2O emissioon; N leostumine põhjavette).

Materjal ja metoodika

Uuritav puistu asub Põlvamaal Holvandis (58°3' N 27°1' E). Lähima meteoroloogiajaama (Võru) andmetel on piirkonna aastane keskmine õhutemperatuur 6 °C, keskmine sademetehulk 653 mm a^{-1} ja keskmine vegetatsiooniperioodi pikkus 191 päeva.

Kultuur rajati 1995. aasta kevadel endisele põllumaale umbes üheaastaste looduslike taimedega, algtihedusega 15 750 ha^{-1}. Prooviala kasvab näivleetunud mullal, ala suurus on 0,08 ha. Puistut on takseeritud igal aastal, enamikel aastatel on hinnatud ka puistu maapealset biomassi mudelpuude meetodil (Borman ja Gordon, 1984; **I**, **V**) (Joonis 1). Puistu leheparameetrid arvutati mudelpuudelt kogutud juhuslikult valitud lehtede pindala ja massiandmete põhjal (**I**).

Jämedate juurte biomassi hindamiseks kaevati välja kolme mudelpuu juurestikud (**I, V**). Peenjuurte ja noodulite tagavara leiti mullamonoliitide põhjal, peenjuurte produktsiooni hinnati sissekasvusilindrite meetodil (**I, V**).

Puidutihedus määrati vastavalt standarditele ISO 3129-1975(E) ja ISO 3131-1975(E), kasutades eeltöödeldud oksavabasid katsekehi (**II**).

Hall-lepiku lämmastikubilansi koostamiseks hinnati nii puistu maapealse (puud, alustaimestik), kui ka maa-aluse osa (puude juured, sh. peenjuured ning alustaimestiku juured) aastast lämmastikunõudlust (**I**; **IV**; **V**), samuti lämmastikuringe peamisi voogusid. Lämmastiku netomineralisatsiooni voogu hinnati maetud kilekottide meetodil (Eno, 1960; Uri *et al.*, 2003; **I**). Lämmastiku leostumise hindamiseks paigaldati alale 10 roostevaba plaatlüsimeetrit, kust veeproove koguti kuuajalise intervalliga. Lämmastiku gaasilise emissioonivoo (N_2O ja N_2) hindamise viis läbi prof. Ülo Manderi töörühm, kasutati vastavalt „suletud kambri" (Denmead ja Raupach, 1993; Hutchinson ja Livingston, 1993) ja heelium-hapniku meetodit (Butterbach-Bahl *et al.*, 1997; Mander *et al.*, 2003).

Et hinnata hall-lepiku mõju kasvukoha mullaomadustele, võeti iga aasta oktoobris kindlatest punktidest üle kogu puistu mullaproove. Proove võeti kuni 50 cm sügavuseni 10 cm kaupa (0–10 cm, 10–20 cm, jne.). Mullaproovidest määrati NPK, pH, orgaanilise aine ja süsiniku sisaldus.

Ülevaateartiklisse (**III**) on koondatud kirjandusandmed Norra, Rootsi, Soome, Eesti, Läti, Leedu, Valgevene ja Loode-Venemaa hall-lepikute biomassi produktsiooni ja majandamissoovituste kohta. Lisaks on artiklis kajastatud seitsme kasvukäigutabeli andmeid, nende hulgas Eesti halli lepa kasvukäigutabel (Raukas, 1930).

Statistilised meetodid

Andmete vastavust normaaljaotusele kontrolliti Lillieforsi ja Shapiro-Wilki testidega (**I, II, IV, V**). Peejuurte biomassi ning lehe eripinna andmeid normaliseeriti logaritm- või juurimisfunktsiooniga (**I**). Keskmiste mitmesel võrdlemisel kasutati Fischer LSD testi, erineva suurusega valimite korral Tukey HSD testi (**I, II, V)**. Andmete erinemisel normaaljaotusest või mittevõrdsete rühmadispersioonide korral rakendati mitteparameetrilist dispersioonanalüüsi (Kruskal-Wallis) (**I, IV**). Puistu takseertunnuste ja biomassi näitajate vaheliste seoste hindamiseks rakendati lineaarseid ning allomeetrilisi mudeleid (**I, II, V**). Selgitamaks tüvesektsiooni mõju puidu tihedusele viidi läbi korduvmõõtmiste dispersioonanalüüs (**II**). Autokorrelatsiooni esinemist peenjuurte andmetel kontrolliti Durbin-Watsoni testiga (**V**). Peenjuurte produktsiooni arvutamisel kasutati Fairly ja Alexandri (1985) otsustusmaatriksit. Peenjuurte aastase käibe leidmiseks sissekasvusilindrites jagati aastane juureproduktsioon (g m^{-2} a^{-1}) peejuurte keskmise biomassiga (g m^{-2}). Peenjuurte efektiivsus leiti tüvemassi aastase produktsiooni ja peenjuurte biomassi jagatisena. Lämmastiku- ja süsinikusisaldus peenjuurtes ja noodulites arvutati nende kaalutud keskmiste kontsentratsioonide ja biomasside alusel (**IV**). Andmetöötluseks kasutati tarkvarapakette STATISTICA 7 (**I, II, IV, V**) ja SAS 8 (**I**). Kõikidel juhtudel oli olulisuse tõenäosus $\alpha = 0{,}05$.

Tulemused ja arutelu

Endisel põllumaal kasvav hall-lepik osutus väga produktiivseks (Tabel 2, Joonis 2). 17-aasta vanuse puistu tüvemass oli 105 t ha^{-1} ja tagavara 265 m^3 ha^{-1} (Joonis 2). Biomassi aastase jooksva juurdekasvu maksimumi saavutas puistu seniste andmete põhjal 16-aasta vanuses, mil tüvemassi produktsioon oli üle 14 t ha^{-1} a^{-1}, mida võib Eesti tingimustes lugeda väga kõrgeks. Kirjandusest leitud lähedase vanusega puistute aastased tüveproduktsioonide maksimumid Loode-Venemaal ja Rootsis jäid suurusjärku 7–8 t ha^{-1} a^{-1} (Utkin *et al.*, 1980; Johansson, 2000). Kirjandusest leitud hall-lepiku tüveproduktsiooni kõrgeim väärtus oli 17 t ha^{-1} a^{-1} 5-aastases väetatud ning niisutatud puistus Rootsis (Granhall ja Verwijst, 1994). Tullus *et al.* (1998) leidsid Eestis kasvava 6-aastase hall-lepiku jooksvaks aastaseks puiduproduktsiooniks (tüvi ja oksad) 14,8 t ha^{-1} a^{-1}. Puistu biomassi aastane produktsioon sõltus oluliselt vegetatsiooniperioodi ilmastikutingimustest, olles selgelt väiksem põuastel aastatel. Töös leitud produktsiooninäitajad ületavad ülevaateartiklis (III) käsitletud kõikide halli lepa kasvukäigutabelite vastavaid väärtusi (Joonis 2).

Lühikese raieringiga majandatava puistu puhul on olulised nii puistu tihedus, kui raieringi optimaalne pikkus, mõlemad mõjutavad puistu produktsioonivõimet. Liiga väikese tiheduse korral ei kasuta puistu kasvukoha potentsiaali täielikult ning seetõttu võib puistu tootlikkus jääda võimalikust madalamaks. Artiklis **III** käsitletud kasvukäigutabelites oli tootlikumate puistute tihedus 15-aasta vanuses suurusjärgus 3300–6500 puud hektaril, 20-aasta vanuses oli vastav näitaja 2300–4500. Uuritud puistu tihedus 17-aastaselt oli 5100 puud hektaril, sellist tihedust võib lugeda lühikese raieringiga majandatava puistu optimaalseks algtiheduseks.

Lühikese raieringiga majandatav puistu on otstarbekas raiuda mahuküpsuse saabumisel – s.o. ajal, kui puistu aastane jooksev juurdekasv (CAI) langeb alla keskmise juurdekasvu (MAI). Mitmete uurijate arvates on halli lepa puhul optimaalne raieringi pikkus 15–20 aastat (Björklund ja Ferm 1982; Rytter, 1995; Lõhmus *et al.*, 1996; Tullus *et al.*, 1998; Rytter *et al.*, 2000; Miežite ja Dreimanis, 2006; Daugavietis *et al.*, 2009; **I**), mis ühtib hästi ka artiklis **III** käsitletud kasvukäigutabelite andmetega. Uuritavas puistus saabus tüveproduktsiooni aastane maksimum 16-aasta vanuses, järgmisel aastal langes see 2,5 korda (Joonis 3). Juurdekasvu nii järsk langus pole tingitud vaid puistu mahuküpsuse saabumisest, vaid on ilmselt suuresti mõjutatud ka vegetatsiooniperioodi ilmastikutingimustest.

Puistu lehemass suurenes alates rajamisest pidevalt kuni 6-aasta vanuseni, mil saavutas stabiilse taseme, jäädes edaspidi vahemikku 3–4 t ha^{-1}, kuid olles väiksem põuastel aastatel. Üksiklehe mass ja pindala olid alati usaldusväärselt suuremad võra kõrgemates osades (**I**).

Tüvepuidu keskmine tihedus endise põllumaa hall-lepikus oli 396 kg m^{-3} (**II**), kusjuures tihedus suurenes usaldusväärselt tüve kõrgemates osades. Samas ei avaldanud puidu tihedusele mõju puu hierarhiline positsioon puistus, st. see ei sõltunud puu rinnasdiameetrist. Kuna praktilises metsanduses on peamiste mõõtühikutena kasutusel mahuühikud, siis on puistu tagavara arvutamiseks biomassi andmete põhjal oluline teada tüvepuidu tihedust. Tabelis 1 toodud väärtuste kohaselt on halli lepa puidu tihedus riigiti väga erinev. Need tulemused kinnitavad Wiemanni ja Williamsoni (2002) teooriat, mille kohaselt puittaimede puidutihedus suureneb kasvukoha laiuskraadi vähenedes.

Puistu maa-alust biomassi hinnati 5-, 10- ja 17-aasta vanuses (**I, IV**). Jämedate juurte ($d > 2$ mm) biomass 10- ja 17-aastases puistus oli vastavalt 8,7 ja 22,3 t ha^{-1}. Peenjuurte biomass ($d \leq 2$ mm) hall-lepikus oli suhteliselt tagasihoidlik ning saavutas maksimumi juba 10-aastases puistus, jäädes alla 1 t ha^{-1}. Boreaalsete metsade keskmiseks peenjuurte biomassiks hinnatakse 5,3 ± 3,2 t ha^{-1} (Finer *et al.*, 2011), uuritud hall-lepiku peenjuurte biomass on sellest ligikaudu kuus korda väiksem. 17-aasta vanuses puistus peenjuurte biomass enam ei suurenenud, vaid oli samas suurusjärgus 10-aasta vanuse puistuga. Kogu uurimisperioodi vältel paiknes ligikaudu pool peenjuurte biomassist mulla ülemises 10 cm kihis. Noodulite biomass puistu vanuse kasvades suurenes, olles 10- ja 17-aastases puistus vastavalt 0,16 ja 0,31 t ha^{-1}. Peenjuurte nekromass oli tõenäoliselt tänu soodsatele lagunemistingimustele kogu puistu arengu jooksul väga väike, jäädes vahemikku 0,02–0,01 t ha^{-1}.

Väga oluline oli hall-lepiku mõju endise põllumaa mullaomadustele. Uuritud 17-aastase kasvuperioodi jooksul muutis hall-lepik usaldusväärselt ($P < 0,05$) mulla lämmastiku- ja süsinikusisaldust. Puistu mulla N varu mulla ülemises 0–10 cm kihis vahetult peale istutamist 1995. aastal oli 1,4 t ha^{-1}, 17-aasta vanuses puistus oli see aga juba 2,1 t ha^{-1}. Endise põllumaa hall-lepik toimis ka olulise süsiniku sidujana, talletades seda nii biomassi kui ka mulda. Mulla C sisaldus mulla ülemises 10 cm kihis oli puistu rajamise ajal 18,2 t ha^{-1}, 17-aastases puistus oli see suurenenud ligi 6 t ha^{-1} võrra. Kuna puistu peenjuurte biomass oli väike (< 1 t ha^{-1}), lehtede aastane produktsioon ja biomass aga 3-4 t ha^{-1}, siis peamine N ja C voog mulda tuli lehevarise kaudu.

Puistu mulda hapestav mõju oli ilme, esimese 7 kasvuaasta jooksul langes pH mulla ülemises 10 cm kihis 1,3 ühiku võrra, hiljem mulla pH stabiliseerus. Selgelt avaldus põuaste aastate pidurdav mõju mulla hapestumise dünaamikale (Joonis 6), mis on tõenäoliselt seotud pärsitud N_2 fikseerimise- ja nitrifikatsiooniprotsessidega.

Sümbiontselt seotud lämmastiku voog (151,5 kg ha^{-1} a^{-1}) kattis ligikaudu kolmveerandi hall-lepiku aastasest lämmastikuvajadusest. Teiseks oluliseks N allikaks oli netomineralisatsioon, mis ülemises 10 cm mullakihis oli 74,1 kg ha^{-1} a^{-1}. N retranslokatsioonivoog lehtedest oli tagasihoidlik (3–10%), suurenedes märgatavalt ebasoodsatel (põuastel) kasvuaastatel.

Väga oluliseks emissioonivooks (74 kg ha^{-1} a^{-1}) osutus N denitrifikatsioon. Enamik gaasilisest lämmastikust emiteerus keskkonnale ohutus N_2 vormis, ohtliku kasvuhoonegaasi N_2O osakaal oli väga väike (0,5 kg ha^{-1} a^{-1}).

N leostumine (15 kg ha^{-1} a^{-1}) moodustas suhteliselt tagasihoidliku osa kogu N bilansist. N leostus põhiliselt orgaanilise- ja nitraatlämmastikuna. Kõige intensiivsem leostumise periood oli sügis, mil vegetatsioon oli lõpetanud N tarbimise, kuid lehevarisest mulda jõudnud lämmastiku jätkuv mineralisatsioon suurendas liikuva nitraatlämmastiku sisaldust mullas. Lüsimeetrid olid paigutatud 40 cm sügavusele ja kuna sügavamas mullakihis (40–50 cm) ilmnes statistiliselt oluline N sisalduse suurenemine (+214 kg 14-aasta jooksul) (Joonis 2 artiklis **IV**), siis suur osa leostunud lämmastikust seoti sügavamas mullakihis.

Kokkuvõte

Endisele põllumaale rajatud halli lepa kultuur oli kõrgproduktiivne ning hall lepp on nii Eestis, kui meie lähiregioonis lühikese raieringiga metsanduse seisukohalt perspektiivne puuliik. Uuritava puistu tootlikkus ületas ülevaateartiklis (**III**) analüüsitud kõikide halli lepa kasvukäigutabelite vastavaid näitajaid. Kultuurpuistu rajamise korral peaks algtihedus jääma vahemikku 3000–6000 puud hektarile ning raieringi soovitatav pikkus oleks ligikaudu 20 aastat.

Hall-lepik on võimeline suure osa oma aastasest lämmastikunõudlusest katma sümbiontse sidumise arvelt, 10-aastases puistus oli sümbiontse N_2 sidumise voog 150 kg ha a^{-1}.

Endisel põllumaal kasvav hall-lepik mõjutas olulisel määral mulla N ja C tagavara. Peamine N ja C voog jõudis mulda lehevarise kaudu, peenjuurte roll jäi väikese biomassi tõttu tagasihoidlikuks. Mulla ülemises 10 cm kihis suurenes N ja C varu 17-aasta jooksul vastavalt 0,67 t ha^{-1} ja 6,30 t ha^{-1}. Põllumaa hall lepik toimis efektiivse C sidujana, akumuleerides seda nii mulda kui biomassi.

Halli lepa mulda hapestav mõju oli ilmne, puistu arengu jooksul langes mulla pH 1,3 ühikut, eriti kiire oli see puistu noores eas, kuid pidurdus 8–9-aasta vanuses ning edaspidi jäi mulla pH stabiilseks.

Hall-lepikute kasvatamisega ei kaasne märkimisväärseid keskkonnariske, N leostumine ning N_2O emissioon olid tagasihoidlikud, vastavalt 15 kg ha^{-1} and 0,5 kg ha^{-1}.

Edasised uurimissuunad

Biomassi, sh. puidu, laialdasem kasutamine energia tootmiseks võib edaspidi tõsta päevakorda nn. energiametsade kasvatamise. Eestis on saab halli leppa pidada perspektiivseks bioenergia ressursiks. Hall-lepikute laialdasem kasvatamine ja majandamine nõuab aga senisest paremaid teadmisi hall-lepikute toimimisest ökosüsteemina, sealhulgas on oluline selgitada lühikese raieringiga majandatavate lepikute mõju kasvukoha süsinikuringele.

Väga vähe uuritud valdkond on lepikute, sh. hall-lepikute maa-aluse osa biomass ja produktsioon, vajalikud on süvendatud teadmised peenjuurte biomassi, produktsiooni ja käibekiiruse kohta.

Kindlasti on halli lepa puistute praktilise majandamise seisukohast oluline välja töötada kohalikele oludele sobivad hall-lepikute kasvukäigutabelid, kuna tänini need sisuliselt puuduvad. A. Raukase 1930. aastal avaldatud kasvukäigutabel on muutunud tingimuste tõttu vananenud. Uus kasvukäigutabel oleks aluseks metsamajanduslike tegevuste planeerimisel ja otsuste tegemisel.

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I

ORIGINAL PUBLICATIONS

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The dynamics of biomass production in relation to foliar and root traits in a grey alder (*Alnus incana* (L.) Moench) plantation on abandoned agricultural land

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Summary

The dynamics of the above-ground biomass production of a grey alder plantation on abandoned farmland was investigated during 11 years after establishment. In the 12-year-old stand, the total biomass of the above-ground part of the stand was 68.8 t dry matter (DM) ha^{-1} and the current annual production (CAP) was 14.0 t DM ha^{-1} year^{-1}. The predicted mean annual increment (MAI) reached is maximum at the age of 16 years, which indicates bulk maturity (the stand age when CAI = MAI) and appropriate rotation time for obtaining maximum biomass production. In the case of short-rotation forestry, initial stand density should not be higher than 6500–6000 trees per hectare. Below-ground biomass accounted for 18 and 16 per cent of total stand biomass at a stand age of 5 and 10 years, respectively. The biomass of the nodules was estimated at 155 ± 63 kg DM ha^{-1} and the biomass of the fine roots was estimated at 870 ± 130 kg DM ha^{-1} in the 10-year-old grey alder stand. Of the fine roots, 80 per cent and almost all nodules were located in the upper 0–20 cm soil layer in both the 5-year-old and the 10-year-old stand. The value of leaf area index increased with stand age, ranging between 1.38 and 5.43 m^2 m^{-2} during the development of the stand. Specific leaf area varied in different years from 11.1 to 13.5 m^2 kg^{-1}.

Introduction

Considering the limited reserves of fossil fuels but also the need to reduce CO_2 emissions, more extensive utilization of biofuels, among them wood, has been discussed worldwide. In conditions of continuously rising fossil fuel prices, energy forestry and renewable energy are likely to gain more importance in the near future. The long-term development plan of the Estonian energy industry foresees a reduction in the use of fossil fuels (primarily oil shale) and an increase in the share of biofuels: by the year 2010, renewable energy must account for 5.1 per cent of total energy consumption instead of the present 0.1 per cent. A precondition for a more extensive establishment and cultivation of energy forests is the existence of available land resources. As the area of arable land fallowed during the last decade in Estonia is ~400 000 ha (Estonian Rural Development Plan), the necessary land resources are available. A part of it is overgrowing naturally, and another part has been afforested. Establishment of fast growing tree species on former arable land would also provide an alternative land use. Consequently, the problems related to the establishment and management of short-rotation forests should been examined.

For short-rotation forestry in Estonia, ecologically and economically the most suitable tree is probably grey alder which is a highly productive, nitrogen fixing and soil-improving species (Saarsalmi *et al.*, 1985; Granhall, 1994; Rytter, 1996a, b; Uri *et al.*, 2002). Grey alder is a widespread tree species in Central and Eastern Europe. In Estonia, it is fourth in terms of forest area (Adermann, 2004). During the last half-century, the area of grey alder stands increased significantly: 15 years ago, the share of grey alder stands was only estimated at 4–5 per cent. A majority of Estonian grey alder stands grow in private forests where they make up 13.7 per cent of all stands; in state forests their share is 1.7 per cent, the total area of grey alder stands is 204 300 ha (Yearbook Forest, 2005).

Replacement of agricultural land by forest brings about various changes in the species composition of the plant cover and biomass both above and below ground. Formation of a forest ecosystem is a multifaceted and intricate process whose important mode of expression is biomass formation and accumulation. Assessment of the production capacity of stands growing on abandoned farmlands is necessary for the scientifically grounded management of these areas as well as for the evaluation of their optimal density and cutting age.

The biomass production of grey alder stands has been studied extensively in the Nordic countries (Saarsalmi *et al.*, 1985; Rytter *et al.*, 1989; Granhall and Verwijst, 1994; Rytter, 1996a, b; Johansson, 1999a, b) and found to be high. In Estonia too several investigations on the biomass production and nutrient status of natural and artificial grey alder stands have been published in the last decade (Lõhmus *et al.*, 1996; Tullus *et al.*, 1996; Uri *et al.*, 2002; Uri *et al.*, 2003a); riparian grey alder stands as potential buffer zones have been dealt with as well (Mander *et al.*, 1997a, b). However, the capacity for biomass production and development of alder stands on arable land has been less studied.

The present pilot study focused on the dynamics of biomass and foliar parameters, as a continuous 11-year time series and below-ground biomass in a 5-year-old stand and in a 10-year-old stand. The results of the study are crucial for a better understanding of the development of stands growing on former agricultural land and for optimization of the rotation period, as well as for compiling carbon accumulation and nutrient budgets (Lõhmus *et al.*, 2002; Uri *et al.*, 2004).

The working hypothesis of the present study was that young grey alder stands on abandoned agricultural land have high capacity for biomass production because of their efficient canopy structure and root systems. We also hypothesize that grey alder should be a promising species for short-rotation forestry because growth of alder stands culminates between 15 and 20 years of growth which is optimal cutting age.

The main aims of the study were as follows:

1. to analyse the dynamics of the above-ground biomass and production of a short-rotation grey alder plantation on former agricultural land in relation to optimal cutting age;
2. to estimate the dynamics of biomass allocation in the above- and below-ground parts of the stand and
3. to analyse the foliar and root traits during the development of a young grey alder stand in relation to productivity.

Materials and methods

Plantation

The study was based on an experimental area located in the south-eastern part of Estonia, Põlva county, 58° 3′ N and 27° 12′ E. According to the data of the Võru meteorological station, which is the closest to the experimental area, mean annual temperature is 6°C, mean precipitation is 653 mm and mean length of the vegetation period is 191 days. The experimental plantation was established on abandoned farmland in spring 1995.

One-year-old transplants of natural origin were used for planting. The survival and growth of the planting stock of different origin is described previously (Uri and Tullus, 1999). The total area of the plantation was 0.08 ha. Before the establishment, the area had been out of use for 2 years. No soil preparation was done before planting. The soil is classified as Eutric Podzoluvisol (according to the Food and Agriculture Organization classification). Initial density was 15 750 trees per hectare. The plantation was established with high primary density proceeding from the high density of natural grey alder stands and considering the experience of energy forestry in the Nordic countries where an initial density of up to 40 000 trees per hectare was used (Elowson and Rytter, 1988; Saarsalmi, 1995). No weed control, fertilization or other treatment was employed. Nor did the study involve any repetitions.

Estimation of above-ground biomass and production

The above-ground biomass and production of the stand was always estimated at the end of August when the process of biomass formation was completed; dimension analysis (Bormann and Gordon, 1984; Uri *et al.*, 2002, 2003a) was used. Biomass estimation for 2000–2005 was considered; the values of survival, growth and biomass production during the first 5 years of the stand have been published earlier (Uri and Tullus, 1999; Uri *et al.*, 2002).

The stem diameter at breast height ($D_{1.3}$) of all trees was measured. The trees were divided into five classes on the basis of $D_{1.3}$, and a model tree was selected randomly from each class. Additionally, a tree was felled from two classes with a larger number of trees. A total of seven model trees were felled every year. In all cases, the sample trees were felled in the middle of the sample plot to avoid the edge effect. The stems of the model trees were divided into five sections: the first section at a height of 0–1.3 m and the second section from a height of 1.3 m up to the living crown; the living crown was divided into three equal layers. In the sections, the living branches were divided into fractions: the leaves, the current year shoots, the older branches and the dead branches were separated. From every fraction, a sub-sample was taken for estimation of dry matter (DM) content as well as for chemical analysis. The samples were dried at 70°C until constant weight and weighed to 0.01 g. The share of the wood and bark of stems was determined. The dry mass of different fractions was calculated for each model tree by multiplying respective fresh mass by the DM ratio (Uri *et al.*, 2002; Uri *et al.*, 2003a).

To estimate the above-ground biomass or leaf area index (LAI) of the plantation, an allometric equation of form (1) provided the best fit:

$$y = a\, D_{1.3}{}^{b}, \qquad (1)$$

where, y is the dependent variable (above-ground biomass of a model tree (g) or leaf area (m^2)), $D_{1.3}$ is the breast height diameter (cm), a and b are parameters (Table 1).

For estimation of biomass of the different compartments (current year shoots, old branches and leaves), we failed to develop a reliable allometric equation ($P > 0.05$). Hence, we used for estimation of the biomass of these compartments at the stand level the percentage distribution of the fractions obtained on the basis of the model trees, which was very stable as proved by earlier investigations (Uri *et al.*, 2002; Uri *et al.*, 2003a, Uri *et al.*, 2007a, b). For the data of 2001–2006, the difference between the mass of the stems found by using an allometric relationship and by using percentage distribution of the fractions remained between 1.2 and 3.3 per cent.

The annual production of the stemwood, bark and branches was calculated as the difference between the masses of the respective fractions for the studied year and for the previous year.

In 2004, above-ground biomass was not estimated, therefore above method in 2005 yielded a production estimate for the two previous years. To

Table 1: Parameter estimates of regression equation (1) for estimation of the above-ground biomass of grey alder

Year	Age, year	a	b	R^2
2000	7	120.40	2.158	0.989
2001	8	77.25	2.431	0.991
2002	9	94.67	2.303	0.994
2003	10	100.99	2.334	0.998
2005	12	50.24	2.707	0.998

a = intercept; b = slope of regression; level of significance $P < 0.0001$ in all cases; R^2 = coefficient of determination.

estimate the share of stemwood production for 2004 and 2005, disks were taken from the middle of all stem sections, dried and polished, and the widths of the annual rings were measured to 0.001 mm using the WINDENDRO (Regent Instruments, Inc.) software. A total of 35 samples were analysed.

Annual wood increment for the sections of the model trees was calculated according to equation (2) (Whittaker and Woodwell, 1968)

$$W_i = W_0(r^2 - (r - i)^2)/r^2 \tag{2}$$

where, W_i is the annual dry mass increment of wood (g), W_0 is the dry mass of wood (g), r is the radius of the analysed disk (mm), i is the thickness of an annual ring (mm).

Using the obtained data, the areas of the annual rings for 2004 and 2005 and the respective shares of annual current increment in stem production were calculated. The relative increments of the fractions of the wood and bark were assumed to be equal.

Estimation of below-ground biomass

The below-ground biomass of the stand was estimated in October 1998 and in October 2003, i.e. for the 5-year-old and for the 10-year-old stand. Two different methods were used: excavation of the root system of the model trees for estimation of the biomass of the stump and the coarse roots (d $\geq$ 2 mm) and soil coring for estimation of the biomass of the fine roots (d < 2 mm) and nodules.

The three model trees were selected randomly according to their diameter distribution, so that the minimum, maximum and average diameter classes were represented. The excavated root systems were carefully washed, placed in plastic bags and separated in the laboratory on the following day into the following fractions: the nodules, d < 2, $2 \leq d < 5$, $5 \leq d < 10$, $d \geq 10$ mm and the stump. For determination of the DM ratio, a subsample was separated from each fraction, and the dried samples were weighed to 0.01 g. The dry mass of each fraction was calculated. The below-ground coarse root (d $\geq$ 2 mm) biomass of the stand was calculated by two different methods (Uri *et al.*, 2002):

1. Use of the above-ground biomass and the average root ratio (share of the root system in the above-ground biomass of the model trees).
2. Use of an allometric relationship between breast height diameter and mass of the root system.

Both methods provided similar results for coarse root biomass.

Root coring was used to estimate the biomass of the nodules and the d < 2 mm roots (Vogt and Persson, 1991). Twenty (1998) or 25 (2003) soil cores were taken randomly over the whole plantation with a cylindrical soil auger (diameter of the cutting edge 48 mm). The soil cores were divided into four 10 cm layers to a depth of 40 cm, placed in polyethylene bags and kept in a refrigerator until processing. Roots and nodules were washed out of the soil cores in the week after sampling. Further, the fractions of the fine roots and the nodules were separated under the binocular microscope and cleaned from soil particles. Dead nodules, dead roots and roots of herbaceous plants were separated as well; however, these fractions were not included in the present study. The samples were dried up to 70°C and weighed to 0.001 g. The soil core data were used for the calculation of the biomass of the fine roots and the nodules per hectare, summing up the average values for the successive soil layers from the soil cores. The share of the fine roots and nodules in the root systems was calculated.

Estimation of foliar parameters

The living crown of the model trees was divided into three equal layers. In the period 1997–2005, annually (except in 2004), 20–25 leaves were randomly taken from each crown layer of the seven model trees (60–75 per model tree) and dried under pressure. Average leaf blade area (ALA) (including the petiole) was measured using the program WINFOLIA (Regent Instruments, Inc.). All measured oven-dry leaf blades were weighed to 0.001 g. Specific leaf area (SLA m^2 kg^{-1}) and LAI (m^2 m^{-2}) were calculated.

The leaf samples were analysed for total Kjeldahl nitrogen. The block digestion and steam distillation methods were used for testing the plant material for nitrogen concentration (Tecator AN 300). The analyses were performed at the Biochemistry Laboratory of the Estonian University of Life Sciences. Annual nitrogen (N) accumulation in leaf biomass (kg ha^{-1} $year^{-1}$) and leaf nitrogen content per leaf unit area (g m^{-2}) were calculated.

Foliar assimilation efficiency (FOE) was calculated by dividing current annual production (CAP) by leaf mass (kg kg^{-1} $year^{-1}$). Photosynthetic nitrogen use efficiency (PNUE) for the above-ground part of the stand was calculated as production per unit of leaf nitrogen (Lambers *et al.*, 1998).

Modelling of the dynamics of stem biomass

Three different growth functions were tested for predicting stand growth:

1 The well-known Richards' (1959) function can be expressed as

$$y = y_{max} \cdot (1 - \exp(-b \cdot t))^c \qquad (3)$$

where, y is the above-ground biomass at stand age (t ha^{-1}),
y_{max} is the maximum above-ground biomass, a function parameter (t ha^{-1}),
b, c are function parameters.

According to the Richards' growth function, the CAP of above-ground biomass can be expressed as

$$CAP = y' = y_{max} \cdot b \cdot c \cdot (1 - \exp(-b \cdot t))^{c-1} \cdot \exp(-b \cdot t)) \qquad (4)$$

2 According to the Hossfeld growth function (5) (Peschel, 1938),

$$y = y_{max} \cdot t^c/(b + t^c) \qquad (5)$$

According to the Hossfeld growth function, CAP can be expressed as

$$CAP = y' = y_{max} \cdot b \cdot c \cdot t^{c-1}/(b + t^c)^2 \qquad (6)$$

3 For modelling of fast growing tree species, the Weibull function (7) (Kiviste, 1987) could prove appropriate:

$$y = y_{max} \cdot (1 - \exp(-b \cdot t^c)) \qquad (7)$$

The Weibull function showed the best fit for the approximation of Orlov's site index tables for deciduous species of vegetative origin (Kiviste, 1987). According to the Weibull growth function, CAP can be expressed as:

$$CAP = y' = y_{max} \cdot b \cdot c\ t^{c-1} \cdot \exp(-b \cdot t^c) \qquad (8)$$

As the stand was planted, stem mass growth was inhibited in the beginning. Hence, for a better fit, a time shift of 1 year was used for all growth functions, which means that variable t in equations (3–8) equals to plantation age minus 1 year.

In this study, the NLIN procedure of SAS the software version 8.2 was used which enabled us to calculate the least squares estimates of the function parameters with standard errors and regression predictions with their confidence limits. The initial values for the estimation of the parameters were obtained from reference books on growth function (Kiviste, 1988; Kiviste *et al.*, 2002).

Statistical methods

Normality of the variables was checked by the Lilliefors and Shapiro–Wilk tests; fine root mass in the soil cores and SLA were normalized by log- or root transformation. The data of model trees were analysed by correlation analysis (Pearson correlation) and regression analysis. For finding allometric relationships (1), $D_{1.3}$ served as the independent variable in all cases. One-way analysis of variance (ANOVA) was used for checking the impact of the crown layer on foliar parameters. The Tukey HSD test in the case of unequal samples sizes was used for multiple comparison of the means. The assumptions of ANOVA were not satisfied to check differences between the fine root samples taken from different parts of the plantation; hence, the non-parametric Kruskal–Wallis analysis of variance was used. Rank correlation analysis (Gamma correlation) was employed to estimate the relationship between tree size and the foliar parameters. The software STATISTICA 7.1 and SAS 8.2 were used and the significance level $\alpha = 0.05$ was accepted in all cases.

Results

Dynamics of above-ground biomass

The decrease in the number of trees during the first decade was very intensive and average height increment was 1.1 m per year. After canopy closure in 1998, the annual mortality of the trees varied between 450 and 2060 trees per hectare (Table 2).

Table 2: The dynamics of the main characteristics of the grey alder stand on former agricultural land for 1995–2005

Year	Age, year	Trees per hectare	Mean height, m	$D_{1.3}$, cm	Basal area, $m^2\ ha^{-1}$	LAI, $m^2\ m^{-2}$	SLA, $m^2\ kg^{-1}$
1995	2	15 750	0.99	–	–	n.e.	n.e.
1996	3	14 020	2.13	–	–	n.e.	n.e.
1997	4	13 110	3.54	1.9	3.71	1.38	11.57
1998	5	12 660	4.62	2.6	6.72	2.24	11.83
1999	6	11 910	5.22	3.1	8.98	1.89	12.82
2000	7	9850	6.12	3.9	11.76	4.05	13.34
2001	8	9350	7.22	4.6	16.36	4.22	13.91
2002	9	8400	8.50	5.2	17.83	1.99	11.97
2003	10	7400	9.48	5.7	19.13	4.01	12.24
2005	12	6780	10.75	6.6	23.20	5.43	13.84

n.e. = not estimated.

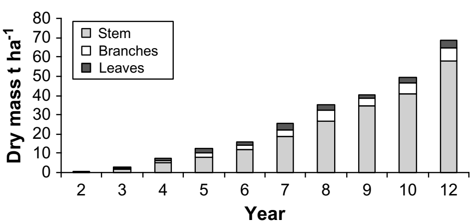

Figure 1. The dynamics of above-ground biomass in the grey alder stand on former agricultural land for 1995–2005.

It was lower in the dry years 1999 and 2002 (450 and 500 trees per hectare, respectively). However, in the 2 years following the dry years, the mortality of the trees was 1.7–4.6 times higher (750–2060 trees ha^{-1} $year^{-1}$). The number of trees per hectare decreased exponentially ($R^2 = 0.98$, $P < 0.001$). Diameter increment was 13–29 per cent less in the dry years than in the years preceding drought years; a reduction in diameter growth was also observed in the 2 years following drought (up to 38 per cent in comparison with the year preceding drought). The stem mass and the total above-ground biomass of the 12-year-old grey alder stand reached 58 and 69 t DM ha^{-1}, respectively (Figure 1).

Because in 2004, model trees were not taken the annual wood production was estimated on the basis of the annual rings of the stem sections. As comparison of the areas of the annual rings of the stems for 2004 and 2005 (64.5 ± 10.5 and 66.4 ± 8.4 mm^2, respectively) did not reveal any significant difference ($P > 0.05$), the CAP of the stemwood for 2004 and 2005 were considered equal and total stemwood production in the 12-year-old stand was estimated at 7.29 t DM ha^{-1} (Table 3). Earlier (1995–1999) production data are published in Uri and Tullus (1999).

A decrease in the production of leaves and branches occurred in the dry years of 1999 and 2002. However, stem production decreased in 2002 and even in 2003 but not in 1999 (Table 3; Uri *et al.*, 2002).

For prediction of optimal cutting age, three different growth functions were tested. The most optimistic predictions of stem biomass were obtained using the Richards' and Hossfeld functions with an asymptote of 207 and 173 t DM ha^{-1}, respectively (Table 4).

The age of maximum mean annual increment (MAI) obtained with the Richards' function exceeds 21 years but, according to the Weibull function, it is 16 years (Table 4). For prediction of stand growth, the Weibull function was selected on the basis of maximum predicted stem volume (Figure 2), which in the case of this function was more realistic (Table 4); this procedure is described in more detail in Discussion.

Below-ground biomass

Using the average share of the root systems of the model trees, below-ground (d ≥ 2 mm) biomass was calculated as 8.7 ± 0.3 t DM ha^{-1} for the 10-year-old stand.

Table 3: CAP (t DM ha^{-1} $year^{-1}$) of the above-ground part in the grey alder stand on former agricultural land for 2000–2005

Year	2000	2001	2002	2003	2005
Age, year	7	8	9	10	12
Stemwood	6.06	7.48	7.18	5.53	7.29
Stembark	0.64	0.71	0.62	0.85	1.07
Current-year shoots	0.99	1.24	0.71	0.66	0.87
Branches (age > 1 year)	0.78	1.37	0.63	1.25	0.77
Leaves	2.99	3.22	1.63	3.04	3.95
Total	11.46	14.02	10.77	11.33	13.95

Table 4: Parameter estimates, RMSE and production characteristics of stem biomass growth functions for the grey alder stand on abandoned agricultural land

	Parameter estimates			RMSE	Age at maximum value, year		Maximum production, t DM ha^{-1}	
Function	y_{max}	b	c	t ha^{-1}	CAP	MAI	CAP	MAI
Richards	206.9	0.0902	2.728	0.77	12.1	21.3	8.48	6.03
Hossfeld	172.9	528.60	2.334	0.75	10.9	18.3	8.31	5.62
Weibull	108.1	0.0032	2.292	0.75	10.6	16.0	8.31	5.37

RMSE, residual mean standard error

Employing regression equation (9), developed on the basis of the data of the three model trees, a similar result, 8.7 t DM ha^{-1}, was obtained.

$$y = 10.84 D_{1.3}{}^{2.598}, \quad (9)$$

$$R^2 = 0.999, P < 0.001,$$

where, y is the mass of the coarse fraction (d > 2 mm) of the below-ground part of tree (g), $D_{1.3}$ is the breast height diameter of tree (cm).

No statistically significant differences appeared between the fine root densities (g m^{-2}) for samples taken from different parts of the plantation (Kruskal–Wallis ANOVA, $P > 0.28$). The average biomass of the nodules in the 10-year-old stand, calculated on the basis of the soil cores, was 156 ± 60 kg DM ha^{-1}. Analysis of the vertical distribution of the living nodules revealed that 81 per cent of them were located in the upper 10 cm soil layer and almost all nodules were contained in the layer with a depth of 0–20 cm.

The mass of the fine roots (d < 2 mm) was estimated at 870 ± 140 kg DM ha^{-1} of which more than half (57 per cent) were located in the upper 10 cm soil layer and 80 per cent were located in the upper 20 cm soil layer (Figure 3). The share of fine roots in total root biomass was estimated as 20 per cent in the 5-year-old stand and 8.9 per cent in the 10-year-old stand. The share of nodules in total root biomass in the 5-year-old stand and in the 10-year-old stand was 6.3 and 1.6 per cent, respectively.

Total below-ground biomass (9.7 t DM ha^{-1}) in the 10-year-old grey alder stand accounted for 16.4 per cent of total stand biomass.

Foliage characteristics

SLA showed a normal distribution for different years; cube root transformation was used for the normalization of the leaf masses and square root transformation was used for normalization of the leaf areas. ALA for the study period (1997–2005) varied from 18.6 to 30.5 cm^2, single leaf mass from 179 to 266 mg and SLA from 11.6 to 13.9 m^2 kg^{-1}. Relative error for all foliar parameters was <5 per cent.

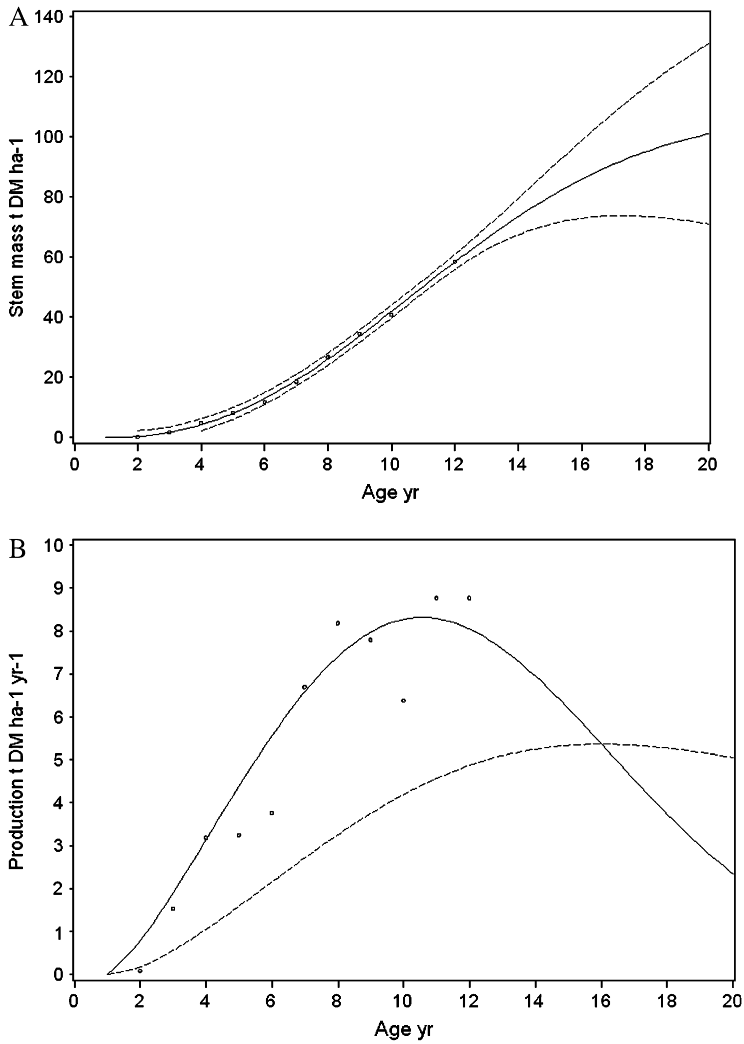

Figure 2. (A) The dynamics of the stem biomass of the stand by measurement data (circles) and by model-based predictions (solid line) with the ~95% confidence intervals for individual predictions (dashed lines); (B) Current annual production (CAI) of the stem biomass of the stand by empirical data (circles) and by model-based prediction (solid line) and predicted mean annual production (dashed line).

Regarding all foliar parameters, the crown layers displayed significant differences ($P < 0.01$). The leaves with the largest blade area and the largest mass were located in the highest layer, both characteristics decreasing towards the lower layers. SLA was significantly larger for the lower crown layers (Tukey test, $P < 0.001$). Although the effect of stand age proved significant for all leaf characteristics (leaf area, leaf mass, SLA), it did not reveal any stand age related trend for any of the characteristics.

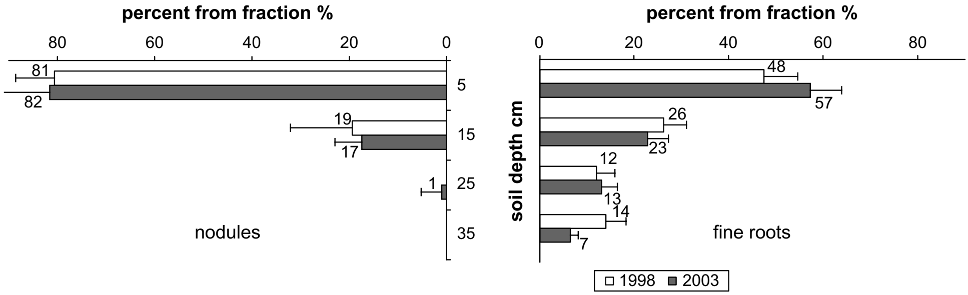

Figure 3. The relative vertical distribution of the fine roots (d < 2mm) and the nodules in the 5-year-old stand and in the 10-year-old grey alder stand on abandoned agricultural land. Bars indicate standard error.

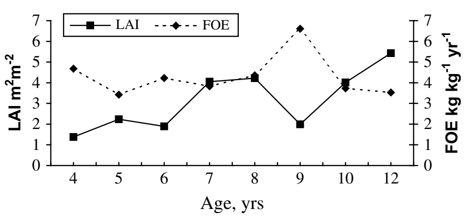

Figure 4. The dynamics of LAI (specific leaf area) and FOE in the grey alder stand on former agricultural land for 1997–2005.

Analysis of the impact of tree size ($D_{1.3}$), i.e. hierarchical position of tree in the stand, on the foliar parameters in different years showed that the effect on single leaf area was insignificant, whereas the effect on single leaf mass proved significant (Gamma correlation, $P < 0.01$). The leaves of the trees with a large diameter also had lower SLA (larger trees have thicker leaves and/or higher tissue density).

The value of LAI for 1997–2005 was estimated as ranging between 1.38 and 5.43 m^2 m^{-2}. The effect of the year on LAI was significant, with LAI decreasing in the unfavourable years (Figure 4). LAI increased with increasing tree age together with the mass of leaves per hectare; LAI and mass of leaves were highly correlated ($R^2 = 0.99$, $P < 0.001$). The correlation between LAI and wood + bark production was less significant ($R^2 = 0.60$, $P < 0.05$).

Leaf N% increased until canopy closure from 2.77 to 3.94 per cent, decreased during the two subsequent years and stabilized thereafter, fluctuating slightly around the 3.5 per cent level. Nitrogen content per leaf area (NLA, g m^{-2}) decreased hyperbolically after canopy closure and stabilized at 2.5 g m^{-2} ($R^2 = 0.98$, $P < 0.001$). FOE for the same period ranged between 3.4 and 6.6 kg kg^{-1} $year^{-1}$ depending on weather conditions in a particular year; PNUE ranged from 87 to 206 kg kg^{-1} $year^{-1}$. There was no significant correlation between FOE and stand age. FOE increased in the dry years (1999 and 2002) when leaf mass and LAI were low (Figure 4). FOE and PNUE were highly correlated ($R^2 = 0.98$, $P > 0.001$).

Discussion

Here, we present the preliminary results based on a chronosequence study of a grey alder stand on abandoned agricultural land, which enabled us to obtain information about stand development and the factors affecting it. Although a large number of young grey alder stands are regenerated on abandoned agricultural land in Estonia, the growth and development of such stands as well as numerous related aspects are yet poorly investigated.

The CAP of above-ground biomass in the 12-year-old grey alder stand was 13.9 t DM ha^{-1} and the annual production of the overbark stems was 8.4 t DM ha^{-1}, which can be considered high. In Estonia, the highest CAP value, 14.8 t DM ha^{-1}, was estimated for a 6-year-old natural grey alder stand (Tullus *et al.*, 1998). The highest reported value of the CAP (stem and branches) of grey alder is 17 t DM ha^{-1} which was estimated for a 5-year-old irrigated and fertilized stand (Granhall and Verwijst, 1994). Rytter *et al.* (1989) found the mean annual production of above-ground woody biomass for a fertilized sphagnum peat bog grey alder stand to be nearly 11 t DM ha^{-1} in the seventh year of growth. According to Saarsalmi *et al.* (1985), total biomass in a 5-year-old grey alder plantation was 31 t ha^{-1} and mean annual production was 8.5 t ha^{-1}. Telenius (1999) found that in 6-year-old grey alder plantations total biomass was 27 t ha^{-1} and annual production 8.6 t ha^{-1}.

One of the most widely discussed issues in short-rotation forestry is optimization of the rotation period, which is related to the maximum value of CAP. The purpose is to maximize biomass production in as short time as possible; a stand should be cut when CAP falls below MAI (bulk maturity). The experience reported in the literature allows us to conclude that in order to maximize the yield, dense plantations with a rotation period of 10–20 years can be recommended (Rytter, 1996b). In a fertilized peat bog experiment, annual woody biomass increased continuously up to 7 years (Rytter *et al.*, 1989). Johansson (1999b) notes that grey alders grow fastest at the age of 5–10 years. In our study, the CAP values for the stems were quite similar for the 8-year-old stand and for the 12-year-old stand, 8.2 and 8.4 t DM ha^{-1} $year^{-1}$, respectively. Thus, the CAP of the 12-year-old-stand had not yet started to decline and optimal cutting age for a grey alder stand growing at such a fertile site is >12 years. CAP fluctuated during the study period depending largely on weather conditions in different years. The summers of 1999 and 2002 were very dry and the decrease in CAP in those years (Figure 2B) can be mainly explained by unfavourable weather conditions. A significant fluctuation in CAP for a grey alder stand in different years was also noted by Rytter (1995).

All three growth functions tested in the study showed an almost similar fit for the stand measurement data. The residual standard error of the Richards' function is slightly higher than that of the Hossfeld or the Weibull function (Table 4). There is no significant difference in the age of maximum CAP (11 or 12 years) calculated by different functions, either. We selected the Weibull function for prediction of the maximum stem biomass of the stand on the basis of maximum stem mass. The respective values calculated according to the Richards and Hossfeld functions are 207 and 173, respectively. According to Hakkila (1971), the basic density of grey alder stems is 361 kg DM m^{-3} and according to Johansson (2005), it is 359 kg DM m^{-3}. We used an average value, i.e. 360 kg DM m^{-3}, in which case the maximum standing stock according to the Richards and Hossfeld functions would be 575 and 480 m^3 ha^{-1}, respectively, which are clearly overestimated values. In different yield tables from Lithuania (Jankauskas), Belarus (Yurkevich) and Latvia (Murnieks) maximum stock values are 349, 286 and 373 m^3 ha^{-1}, respectively (Krigul, 1971). In an overmature riparian grey alder stand, stem biomass was estimated at 105 t DM ha^{-1} (Lõhmus *et al.*, 1996). Hence, from the viewpoint of prediction of maximum stem mass, the Weibull function shows the best fit. This explains why, for the prediction of stem biomass, using the Weibull function – with the age of a MAI maximum of 16 years (Table 4, Figure 2B) – is more plausible compared with the Richards or the Hossfeld function. According to Rytter (1996b), MAI culminated at stand age 13 years and, according to Raukas (1930), at about 15 years.

Another important issue in silviculture and in short-rotation forestry is optimal initial stand density, on which depend biomass production per area unit, on the one hand, and the cost of the establishment of the plantation on the other. In the 12-year-old stand, 6780 trees per hectare had survived. Johansson (1999b) pointed out that in a dense stand growing at a fertile site, especially on former farmland, thinning should be done at a young age (<5 year) and the number of stems should not exceed 2000 trees per hectare if the stand is managed for timber production. However, such density seems to be too low for the 5-year-old short-rotation grey alder stand, as biomass production per area unit depends largely on the number of stems.

In a thinned grey alder stand in Sweden, there were 6400 stems per hectare and in an unthinned stand of the same age, the number of trees was 22 500 per hectare after 13 years (Rytter, 1995). At the same time, the total production of above-ground woody biomass (standing + thinned) was not significantly different in the thinned stand and in the unthinned stand (Rytter, 1995). However, mean diameter was significantly larger in the thinned stand. In the present study, the initial density of the stand was 15 750 trees per hectare. In the 12-year-old stand, when CAP had not yet started to decrease, the number of surviving trees was 6800. Considering this, we recommend that a short-rotation grey alder plantation for bioenergy should be planted with a density not higher than 6000–6500 plants per hectare.

The above-ground and below-ground parts of the stand developed proportionally, the biomass of the coarse fractions of the below-ground part in the 10-year-old stand was estimated at 8.7 ± 0.3 t DM ha^{-1} and in the 5-year-old stand at 1.97 t DM ha^{-1} (Uri *et al.*, 2002), which formed 19.1 and 18.7 per cent of the biomass of the above-ground part, respectively.

The increase in the biomass of the fine roots from the age 5 years to the age 10 years was modest, from 550 ± 105 to 870 ± 140 kg DM ha^{-1}. Total below-ground biomass (9.7 t DM ha^{-1}) in the 10-year-old grey alder stand was smaller than the relevant values reported in the literature. According to Saarsalmi *et al.*, (1985), the mean biomass of 4-year-old alder roots in a coppiced stand was 5.2–6.1 t ha^{-1} and the mean biomass of 8-year-old alder roots in a coppiced stand was 12 t ha^{-1} (Saarsalmi *et al.*, 1991). The impact of vegetative regeneration on root biomass is not excluded.

At the same time, the biomass and vertical distribution of the nodules remained unchanged during 5 years (Figure 3), being 156 ± 60 kg DM ha^{-1} in the 10-year-old stand and 169 ± 76 kg DM ha^{-1} in the 5-year-old stand (Uri *et al.*, 2002). Both estimations are smaller than it was in 4-year-old grey alder coppiced stand in Finland (250–290 kg ha^{-1}) (Saarsalmi *et al.*, 1985). It can be concluded that the 5-year-old grey alder stand on former farmland has already formed an optimal biomass of the nodules to ensure sufficient symbiotic N_2 fixation. The growing site is sufficiently fertile as most of the annual nitrogen demand in this stand is covered by net nitrogen mineralization (Uri *et al.*, 2003b) and, most probably, there is no need for a larger biomass of the nodules. The short root-specific area (m^2 kg^{-1}) estimated in our earlier study in 1999 was 1.5 times higher (103 m^2 kg^{-1}) in the studied stand than in natural riparian alder forests, which indicates the use of an intensive strategy for improvement of mineral nutrition (Lõhmus *et al.*, 2006). However, the relative share of the fine roots and nodules in total below-ground biomass decreased in 5 years. The proportion of the fine roots in the below-ground part of the stand was more than two times smaller, and the share of nodules was four times smaller in the 10-year-old stand than in the 5-year-old plantation. The proportion of the below-ground part in total biomass in the present study (16 per cent) remained within the limits of 13–19 per cent for cold-temperate broadleaved deciduous forests (Vogt *et al.*, 1996).

Leaf mass increased up to the sixth year of the plantation and stabilized thereafter. Its average value was ~3 to 4 t DM ha^{-1}, except for the extremely dry year of 2002, for which leaf mass was approximately two times smaller. It can be supposed that such leaf mass is optimal for a stand of given density. The leaf mass of 6- to 18-year-old natural grey alder stands in Estonia was in the range 2.9–4.8 t DM ha^{-1} (H. Tullus, unpublished data). In Sweden, the leaf mass of older grey alder stands varied between 2.7 and 6.2 t ha^{-1} (Johansson, 1999a). In Finland, the leaf mass of older grey alder stands varied between 1.7 and 2.9 t ha^{-1} (Saarsalmi and Mälkönen, 1989). The shares of leaf mass in total above-ground biomass in the 5-year-old stand and the 10-year-old stand were quite similar, 29 and 27 per cent, respectively. Hence, a sufficiently large and efficient foliage is already formed at a young age.

Average SLA (12.0 m^2 kg^{-1}) in 1997–2005 is in good accordance with the data published by Johansson (1999a) (12.8 m^2 kg^{-1}). As a rule, SLA is related to the photosynthesizing capacity of the tree and to leaf nutrient concentration (Wright *et al.*, 2002). After canopy closure, there was strong hyperbolic relationship between NLA and stand age. SLA is a highly plastic characteristic depending on many factors including leaf age and growth conditions. Plants with large SLA can have high growth rate but lower tolerance of nutrient and water deficit (Marron *et al.*, 2003). The value of SLA depended on the crown layer and was higher for the lower layers where the leaves are thinner (shade leaves). Light decreases exponentially in the crown, to which the leaves respond with morphological adaptations. The leaves growing in shade are thinner, which favours light capture in situations where light is limiting, as the light receiving area per mass unit is larger and shading is lower inside the leaf (Reich *et al.*, 1997).

In our study, the effect of stand age proved significant for all studied leaf characteristics (leaf area, leaf mass, SLA) but there was no significant trend for any of the characteristics in relation to stand age. However, Kull and Niinemets (1993) pointed out that SLA decreases with increasing tree age. Most probably, increase in SLA occurs during stand development up to middle age, followed by a subsequent decrease with increasing age up to maturity.

LAI increased with age (Figure 4). The exceptional year was 2002 which was unusually dry. The obtained values remain in the range reported in the literature (Lõhmus *et al.*, 1996). According to a study carried out in Sweden (Johansson, 1999a), mean LAI for grey alder stands aged up to 21 years ranged from 1.61 to 5.05 $m^2 m^{-2}$.

For calculating FOE and PNUE, we assumed that the maximum of total biomass as well as that of foliage biomass occur at the end of the vegetation period, i.e. in the middle or at the end of August. On the bases of N concentration and foliage biomass, it is possible to estimate bulk N accumulated in the foliage, and as the annual production of the leaves and foliage biomass are equal, the amount of the nitrogen accumulated in foliage biomass is equal to annual N demand. As the retranslocation flux of N from the leaves in alders is low (Dawson and Funk, 1981; Lõhmus *et al.*, 2002; Uri *et al.*, 2002), no marked changes in the amount of nitrogen invested in the foliage take place in August.

After canopy closure, FOE and PNUE were the highest in the years when LAI was at minimum, i.e. the years with unfavourable weather conditions (drought). When leaf mass and LAI decrease, the assimilation capacity of the leaves increases in order to ensure growth and development of trees. Hence, unfavourable weather conditions in the dry years were partly compensated for by higher FOE and higher nitrogen productivity.

Conclusions

Biomass production in the studied stand was high, which shows that short-rotation grey alder stand on abandoned agricultural land can be a promising source of bioenergy. High productivity is ensured by an effective structure of the crown and the root systems, as well as by the nitrogen utilization and assimilation efficiency of the foliage. As the present investigation is a pilot study, short-rotation grey alder stands growing on abandoned agricultural land with different soils and densities deserve further research.

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Conflict of Interest Statement

None declared.

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Stemwood Density in Young Grey Alder (*Alnus incana* (L.) Moench) and Hybrid Alder (*Alnus hybrida* A. Br.) Stands Growing on Abandoned Agricultural Land

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Abstract

The aim of the study was to determine the density of oven dry stemwood (moisture content 0%) of two fast-growing tree species, grey alder (*Alnus incana* (L.) Moench) and hybrid alder (*Alnus hybrida* A. Br.), growing on abandoned agricultural land. The study is based on two 16-year-old experimental stands located in Southern Estonia (N 58°32 E 27°12). The average stemwood density of grey and hybrid alder was 396±32 kg m^{-3} (average ± st. error) and 427±29 kg m^{-3}, respectively.

For grey alder, the impact of stem height section on stemwood density was significant in all cases ($p<0.005$); it was higher in the upper stem sections. A similar trend was revealed for hybrid alder.

There was no correlation between breast height diameter and average stemwood density either for grey alder or for hybrid alder.

Key words: grey alder, hybrid alder, stemwood density, abandoned agricultural land

Introduction

Considering the limited reserves of fossil fuels but also the need to reduce CO_2 emissions, more extensive utilization of biofuels, among them wood, has been discussed worldwide. In the conditions of continuously rising prices of fossil fuels, energy forestry and renewable energy will gain more importance in the nearest future. The long-term development plan of the Estonian energy industry foresees a reduction in the use of fossil fuels (primarily oil shale) and an increase in the share of biofuels.

In connection with the more intensive use of woody biomass, the issues of biomass production and short-rotation forestry have been added to the agenda. In recent time several research projects have been carried out and new data about the biomass production of different tree species have been reported. Among them several studies demonstrate that grey alder (*A. incana* (L.) Moench) is a promising fast-growing tree species for short-rotation forestry in the Nordic and Baltic countries (Granhall and Verwjist 1994, Saarsalmi 1995, Rytter 1996, Telenius 1999, Miezite 2008, Uri et al. 2002, 2009). According to several research results this species is highly productive both on mineral and organic soils (Granhall and Verwjist 1994, Saarsalmi 1995, Lõhmus et al. 1996, Rytter 1996, Tullus et al. 1998, Telenius 1999, Uri et al. 2009).

However, in scientific publications the values of biomass production are usually expressed in weight units (t ha^{-1}; kg ha^{-1}) while in practical forestry stem volume units (m^3 ha^{-1}) are applied. For converting data from mass units to volume units, or conversely, determination of an appropriate wood density value is essential.

Data on grey alder wood densities are highly variable; the values reported by Nordic authors are quite low (Hakkila 1970, Björklund and Ferm 1982, Johansson 2005) compared with those reported from the Baltic countries (mainly Latvia) (Table 3). The empirical values of grey alder wood density from Estonia are practically missing with the exception of only a few preliminary results (Keedus and Uri 1997). Thus there is a need for empirically substantiated values of grey alder stemwood density which is inherent in the local region.

While grey alder and black alder (*A. glutinosa*) are widespread tree species in the northern hemisphere, hybrid alder (*Alnus incana x Alnus glutinosa*) is rather rare in the nature in Estonia as well as in the other Baltic countries with only a few reported habitats (Hainla 1971, 1979, Pirag 1962, Kundzins 1969). Data on the growth and yield of hybrid alder are also quite scarce in the literature. However, some results show that its growth in natural conditions can be more rapid than the growth of grey alder or black alder (Pirag 1962, Kundzins 1969). Granhall (1982) suggests that hybrid alder can be considered a promising species in short-rotation forestry. Hybrid alder might also be potentially interesting for timber industry, as the quality of its wood is intermediate between that of grey alder and black alder, while the increment of the wood is larger compared with that of black alder (Pirag 1962).

Species	Location	Area, ha	Age, y	Stand density, ha^{-1}	Soil	$D_{1,3}$, cm	Height, m	Basal area, $m^2\ ha^{-1}$
Grey alder	58°3' 27°1'	0.1	16	5400	Eutric Podzoluvisol	9.3±2.9	13.9±2.1	35.2
Hybrid alder		0.2		3600		9.4±3.1	13.1 ±0.7	24.8

Table 1. Description of the study sites (average ± st. deviation)

In the last decade some experimental plantations of hybrid alder were established in Estonia, on the basis of which the growth dynamics and biomass production of this tree species have been described (Uri and Tullus 1999, Uri et al. 2003). Regarding stemwood density, only a few results have been reported about hybrid alder until recent time (Pirag 1962) and this issue has not been studied earlier in Estonia.

Establishment of plantations of fast-growing tree species for biomass production, preferably on abandoned agricultural land, will be the prospect of the nearest future. Thus studies focusing on grey alder stands growing on abandoned farmland represent innovative research.

The main aims of the present study were:

– to estimate knot free stemwood density in young grey alder and hybrid alder stands growing on former agricultural land;

– to analyse the effect of tree height section and breast height diameter on stemwood density of grey alder and hybrid alder.

Material and methods

Stem samples of grey alder and hybrid alder were collected from two plantations established in 1995 and 1996, respectively. Both stands are growing on fertile former agricultural land (Table 1) and the results about their biomass production have been published earlier (Uri et al. 2002, 2009). When the expression "stemwood density" is used in current paper, oven dry (moisture content 0%) stemwood density is considered.

Estimation of wood density

The stem diameter at breast height ($D_{1.3}$) of all trees was measured in both stands in the September of 2009. The trees were divided into five classes on the basis of $D_{1.3}$ and a model tree was selected randomly from each class. An additional tree was felled from two classes with a larger number of trees in order to have a more representative sample and valid data. Altogether seven model trees were felled from both stands. The stems of the model trees were divided into five sections: the fifth section at a height of 0 to 1.3 m, the fourth section from a height of 1.3 m up to the living crown. The living crown was divided into three layers of equal length; the sections were numbered from three to one, as the third section being the lowermost. For estimating wood densities of different stem sections, subsamples with a length of 50 cm were sawn from the middle part of stem sections 5, 4 and 3. The height of the third section was dependent on the beginning of the living crown. It was slightly higher for grey alder than for hybrid alder, varying from 7.9 to 10.0 m and from 7.0 to 9.2 m, respectively. The stem samples were sawn into board in a wood processing laboratory and dried at room temperature until the moisture content equilibrium of the indoor air which was detected by the successive weightings until reaching the constant mass. After the samples were planed and calibrated, as many knot- and bark-free test pieces (3x2x2 cm) as possible from each test subsample were sawn in accordance with ISO 3129-1975 (E), ISO 3131-1975 (E). All test pieces were identified with a number, then dried in the oven at 102°C until constant dry mass. The test pieces were measured with an electronic caliper to 0.01 mm and weighed to 0.01 g. The volume (1) and density (2) of each oven dry test piece was calculated as follows:

$$V=abc, \quad (1)$$

where *a, b* and *c* are the dimensions of test pieces (mm),

$$\rho=V/m, \quad (2)$$

where *V* is the volume of the test pieces (cm^3) and *m* is the mass of test pieces (g).

Statistical methods

Normality of data was tested with the Lilliefors and Shapiro-Wilk tests. Repeated Measures Analysis of Variance was used for checking the impact of stem section on stemwood densities. The assumptions of ANOVA were full filled in all cases. The Tukey HSD test in the case of unequal samples size and Ficher's LSD test were used for multiple comparison of means. Linear and allometric models were employed for estimating relationships between tree dimensions ($D_{1.3}$) and wood densities. The software STATISTICA 7.1 was employed and the significance level a=0.05 was accepted in all cases.

Results

Average stemwood density and effect of tree height section

The average stemwood densities of hybrid alder were significantly higher than the respective values of grey alder ($p<0.05$; Unequal N HSD test).

The stemwood density of grey alder and hybrid alder was 396±32 kg m^{-3} and 427±29 kg m^{-3}, respectively. Average difference between the stemwood densities of the two species was 7.3%.

The wood density of hybrid alder can be considered vertically more homogeneous compared to grey alder. The intersectional variance of hybrid alder stemwood densities is roughly half as big as for the same values of grey alder (Table 2). The breast height diameter of sample trees had no effect on wood densities for either species.

For grey alder, the effect of stem section was significant ($p<0.0001$). The analysis also indicated that effect of repetitions is not significant ($p>0.9$), i.e. there are no differences between repeated measurements within one section.

Table 2. Stemwood densities of grey alder and hybrid alder in different height sections. Section V - 0 to 1.3 m; Section IV - 1.3 to the living crown; Section III - the lowermost third of the living crown

Species	Stem section	N
	III	
Grey alder	464 a* ± 9	24
Hybrid alder	460 a ± 16	23
	IV	
Grey alder	405 b ± 19	83
Hybrid alder	429 a ± 25	89
	V	
Grey alder	376 c ± 19	117
Hybrid alder	415 b ± 26	108

*- Letters indicate significant difference ($p<0.05$)

According to the Tukey HSD test average stemwood densities differ significantly between the sections. The highest wood densities were determined in the highest measured section (section no. 3) of the stem and the lowest densities were found in the lowermost part of the stem (Table 2). All differences between the wood densities of different sections of grey alder are significant ($p<0.05$).

Stem section did not affect wood densities of hybrid alder ($p=0.07$). Wood density was only significantly different between section 3 and section 5 ($p<0.05$; Fisher's LSD test) (Figure 1). Differences between the sections in percentages are approximately twice smaller for hybrid alder than for grey alder.

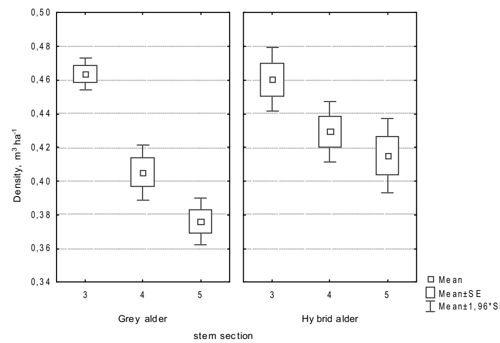


Figure 1. Average stemwood density of grey alder and hybrid alder in different stem sections (section 3 is the highest and section 5 is the lowest)

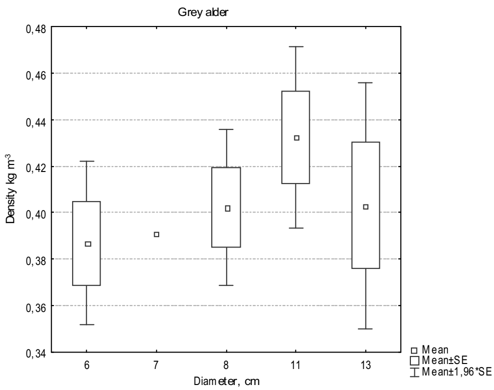
Effect of tree dimensions

Linear regression analysis was applied to study the effect of tree breast height diameter on stemwood densities. The breast height diameter did not affect stemwood density. The study failed to demonstrate any evident trend in stemwood densities for trees belonging to different diameter classes (Figure 2).

Discussions

The average stemwood densities of grey alder found in this study are in good accordance with earlier results reported in the literature (Table 3). Wiemann and Williamson (2002) suggested that the mean wood specific gravity of angiosperms gradually increases with decreasing latitude. Average wood densities reported from Nordic countries (Finland, Norway, Sweden) are lower than those reported from more southern countries (Latvia) (Table 3), which is most probably related to higher mean annual temperature and the longer vegetation period.

Data about the stemwood density of grey alder are relevant for biomass research. In recent time, several studies on the biomass productivity of grey alder have been carried out in Estonia. However, as a rule, all scientific estimates in these studies are expressed in mass-based units (t ha^{-1} or kg ha^{-1}). For comparing the obtained biomass estimates with the data of the



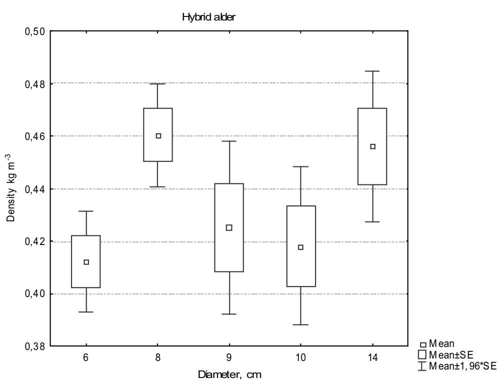


Figure 2. Average stemwood density of grey alder and hybrid alder trees with a different breast height diameter

Table 3. Average stemwood densities of grey alder on the basis of different literature sources

Country	Density kg m^{-3}	Author
Norway	369	Stemsrud (1964)
	365	Nagoda (1966)
	340 (324...358)	Vadla (1999)
Sweden	359 (230...440)	Johansson (2005)
Finland	361	Hakkila (1970)
	353	Björklund & Ferm (1982)
Estonia	384	Keedus, Uri (1997)
Latvia	432...574	Vanins (1950)
	420	Pirag, 1962
	420...630	Draudiņš, Bekeris (1979)
	432...458	Klevinska, Bikova (1999)
	447 (388...506)	Miezite (2008)

average increment of Estonian grey alder stands, or with the data of yield tables, an appropriate stemwood density value is required. Already quite slight variability in the density value used affects the obtained result considerably. For example, the annual current production (CAI) of stem mass in a 15-year-old grey alder stand studied by us was 14.2 t DM ha^{-1} yr^{-1}. When converting this result to volume units and using the oven dry stemwood density value obtained in this study (396 kg m^{-3}), the annual stand stemwood increment will be 35.8m^{3} ha^{-1}. However, when using the wood density value reported from Sweden (359 kg m^{-3}), CAI would be 39.5 m^{3} ha^{-1}, and basing on oven dry grey alder wood density data from Latvia (Miezite and Dreimanis 2006) CAI would be 30.9 m^{3} ha^{-1}.

In published literature, the data about oven dry wood density are scarce; mostly the data of basic density are reported. Still, results of oven dry wood density of common alder, silver birch and European aspen, reported in the Estonian wood science handbook (Puiduteadus 2006) are 490, 600 and 470 kg m^{-3}, respectively.

Current study reports the results about the wood densities of grey- and hybrid alder which are estimated on the basis of one stand per species. Both stands are thoroughly investigated and the results have been published throughout the years (Uri and Tullus 1999, Uri 2000, Uri et al. 2002, Uri et al. 2003ab, Aosaar and Uri 2008, Uri et al. 2009). However, no studies about wood properties have been carried out. In the case of hybrid alder only few planted stands are growing in Estonia at all. Due to the restraint of single sample area per species, the present results are applicable mainly on a regional level. While previous data for grey- and hybrid alder wood density for Estonia are practically missing, the results are valuable both for practical and scientific aspects.

In both grey alder and hybrid alder, stemwood densities increased in the upper stem sections. However, the difference in densities between the stem sections was statistically significant for grey alder but not for hybrid alder. The highest densities occurred in the upper part of the stem, which is in good accordance with the results of other studies (Nagoda 1968, Björklund and Ferm 1982, Miezite 2008). One possible reason for this may be the gradual change in the proportions of late- and earlywood. In younger age the width of the annual rings was large due to rapid tree growth and the relative proportion of less dense earlywood was big compared to the proportion of denser latewood. Later on, when the rate of tree growth started to decelerate, the share of latewood in the annual rings increased and also wood density started to gradually increase.

Data about the wood properties of hybrid alder in the literature are scarce (Pirag 1962). Earlier studies have pointed out that the wood properties, including wood density, of this tree species are intermediate between the parental species (grey alder and black alder) (Pirag 1962). According to Pirag (1962), stemwood density was 420 kg m^{-3} for grey alder and 520…540 kg m^{-3} for black alder; the density of hybrid alder wood was 500 kg m^{-3}.

In hybrid alder, the distribution of wood densities is vertically less variable than in grey alder. A statistically significant difference was only revealed between the third and the fifth sections, i.e. the lowest and the highest trunk sections studied. The growth strategy of hybrid alder differs from that of grey alder. Hybrid alder achieves its maximum stemwood increment later than grey alder, hence, changes in the proportions of early- and latewood are not so drastic. This could explain the more homogeneous vertical wood density distribution in hybrid alder.

In the present study no correlation was found between average stemwood densities and breast height diameter for either studied tree species. Also, the same average density values would be appropriate both for small and large trees, which would simplify the practical use of average wood density value.

Conclusions

Average stemwood density of hybrid alder is significantly higher than that of grey alder's. Stemwood densities determined of grey alder increase gradually from the stump towards the crown, but not that of hybrid alder. The wood of hybrid alder is vertically more homogeneous than the wood of grey alder. There is no correlation between breast height diameter of tree and stemwood densities. For Estonian forestry practice, the recommended oven dry stemwood density would be 396 kg m^{-3} for grey alder and 427 kg m^{-3} for hybrid alder.

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ПЛОТНОСТЬ СТВОЛОВОЙ ДРЕВЕСИНЫ В МОЛОДЫХ ДРЕВОСТОЯХ СЕРОЙ (*ALNUS INCANA* (L.) MOENCH) И ГИБРИДНОЙ ОЛЬХИ (*ALNUS HYBRIDA* A. BR.), РАСТУЩИХ НА ЗАБРОШЕННЫХ СЕЛЬСКОХОЗЯЙСТВЕННЫХ ЗЕМЛЯХ

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Резюме

Основной целью исследования было определить плотность абсолютно сухой стволовой древесины (влажность 0%) двух быстрорастущих древесных пород, серой ольхи (*Alnus incana* (L.) Moench) и гибридной ольхи (*Alnus hybrida* A. Br.), растущих на заброшенных сельскохозяйственных земелях. Исследование проводилось в двух 16-летних экспериментальных древостоях, расположенных в Южной Эстонии (N 58° 3’ E 27° 1’). Средняя плотность абсолютно сухой стволовой древесины серой ольхи была 396 ± 32 кг м$^{-3}$ Средняя плотность стволовой древесины гибридной ольхи превысила соответствующее значение серой ольхи. Средняя плотность абсолютно сухой гибридной ольхи была 427±29 кг м$^{-3}$.

У серой ольхи плотность стволовой древесины была больше в верхних частях ствола. Статистически значимая зависимость плотности древесины от расположения секции ствола наблюдалась во всех случаях (p <0,005). Аналогичная тенденция была выявлена для гибридной ольхи, однако статистические различия между разными секциями ствола не подтвердились.

Величина диаметра на высоте груди не имела существенного влияния на плотность древесины во всех случаях. Корреляции между диаметром на высоте груди и средней плотностью древесины ни у серой и ни у гибридной ольхи не обнаружено.

Ключевые слова: серая ольха, гибридная ольха, плотность стволавой древесины, заброшенная сельскохозяйственная земля

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Review

Biomass production potential of grey alder (*Alnus incana* (L.) Moench.) in Scandinavia and Eastern Europe: A review

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ABSTRACT

Owing to its ability to produce large amounts of biomass in a short period of time, grey alder can be considered to be a prospective tree species for short-rotation forestry (SRF) in Eastern Europe and the Nordic countries. Relatively scanty data is available about grey alder yield and growth dynamics. Seven yield-tables from six countries and several published studies have been included in this review. The main aim of the review was to sum up and analyze published data; to evaluate the potential for biomass production and to summarize the existing relevant knowledge for giving recommendations about the optimal principles on managing alder stands. According to different yield-tables, the mean annual increment (MAI) of 20-year-old stands varied from 2.56 m^3 ha^{-1} to 4.75 m^3 ha^{-1} (dry matter). In favourable conditions, the growth of alder stands can be rapid and biomass production high. The highest woody biomass of annual production reported in literature amounts to 17 t ha^{-1} y^{-1}. A rotation length of 15…20 years is recommended by the majority of authors. The rotation period is longer in northern countries (Norway, Finland) than in southern countries. According to yield-tables, it coincides with the start of the decrease in MAI in most cases. Approximately 60 t ha^{-1}–90 t ha^{-1} of stemwood can be produced during one rotation. The density of the natural grey alder stand is typically very high. The optimal initial density of grey alder may not exceed 10,000 ha^{-1} in the case of plantations and the optimal number of trees per hectare before harvesting should range between 3000 ha^{-1} and 6000 ha^{-1}.

1. Introduction

The immediate goal in the renewable energy sector of the European Union is to increase the share of the energy generated from non-fossil sources to 20% by 2020 [1]. The use of green biomass for energy production instead of fossil fuels is one way of reducing greenhouse gas (GHG) emissions. Future land use scenarios for Europe foresee a significant increase in energy crop areas [2]. Short-rotation forestry (SRF) is regarded as a silvicultural practice employing high-density plantations of fast-growing tree species on fertile land [3]. Such plantations may have great potential as a prospective CO_2 emission-free replacement for fossil fuel [4,5]. SRF plantations are gaining popularity in many countries owing to their efficient land use in combination with an increasing demand for renewable energy sources and additional possibilities for environmental control [6,7]. The most suitable areas for bioenergy

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production are abandoned agriculture lands, which cover globally 385 mha–472 mha [8]. A significant increase in the area of abandoned agricultural lands due to changes in the political and economic situation has occurred in Eastern Europe [9–12]. Hence, agricultural land used for the cultivation of fast-growing tree species may become an important supplier of energy that has a marginal impact on the increasing levels of GHG in the atmosphere.

The grey alder is naturally widely distributed in the Baltic countries and in Scandinavia. In Estonia, the growing stock of grey alder is 31 hm^3 [13]; in Latvia 31 hm^3 [14]; in Lithuania 21 hm^3 [15]; in Sweden 49 hm^3 [16]. According to Yearbook Forest 2009, the growing stock and area of grey alder stands in Estonia has been increasing continually for more than half a century. During the few previous decades, growth has been rapid due to economic changes (collapse of the USSR caused a drastic decline in agricultural activities in the 1990s). Similar trends can be noted in Latvia and Lithuania. The importance of the grey alder has increased – not only in terms of viewing it as wood for fuel but also as a timber source.

Agricultural areas left out of use are rapidly occupied by different pioneer tree species, alders among them. The growth of alders on former arable lands has been reported in many countries: Sweden [17], Finland [18], Russia [19], Norway [20], Estonia [21], France [22], Korea [23], Latvia [24].

Furthermore, alders as pioneer species can successfully be used for the forestation of mining areas [25,26]. The grey alder has high biomass production ability both on mineral and organic soils [17,18,27–30] and is a promising tree species for SRF in Estonia [21,31,32].

Studies have been published about the biomass production capability of other possible SRF species in Scandinavia and Baltic countries, mainly birch, hybrid aspen, and common alder. According to several researches [33–37], the biomass production capability of the species listed varies remarkably.

Grey alder also has some essential silvicultural advantages, making it a promising species for short-rotation forestry. Grey alder seedlings withstand direct sunlight and frost; they only display a few pests and diseases [38]. After felling, a new alder generation emerges both from rootsuckers and stump sprouts, owing to which, the artificial reforestation of clear-cuts is not needed [39]. Due to its symbiotic nitrogen fixation capacity, grey alder is able to cover a large proportion of its annual nitrogen demand with nitrogen from the atmosphere [40–42] and, compared to other short-rotation energy forest tree species, the need for expensive nitrogen fertilization will be smaller or lacking altogether.

In order to generalize the existing knowledge and to give some recommendations about the optimal methods for managing grey alder stands in Northern and Eastern Europe, it is important to sum up and analyze the data published. In the present paper, the growth, yield and production capacity of grey alder stands growing in different regions and at various sites are reviewed. The main objectives of the present paper are: (1) to estimate the potential biomass production capacity of grey alder stands growing at different sites in Northern and Eastern Europe; (2) to compare and characterize grey alder yield-tables from different countries; (3) to investigate some management issues (optimal rotation length; initial density) of grey alder stands.

2. Material and methods

The study is based on the data from grey alder yield-tables and on relevant scientific publications. For a better overview, the data from yield-tables and individual research papers were presented in separate chapters. The growth dynamics of grey alder stands in Scandinavia, the Baltic countries and Belarus is studied on the basis of yield-tables. Several yield-tables are available for the grey alder: Latvia [43,44]; Estonia [45]; Finland [46]; Norway [47]; Lithuania (Jankauskas) [48]; Belarus (Yurkevich) [48]. The production capacity of grey alder was studied on the basis of various research papers from Nordic and Baltic countries ([29,31,32,49–56],etc.). Still, information about the growth dynamics and production capacity of grey alder is scarce. Various yield-tables and data available in literature (listed above) were used to describe and compare the growth patterns of grey alder mainly in the Nordic and Baltic countries.

The highest quality classes (with the highest site index) in the yield-tables were compared in all cases. As a rule, the data in the yield-tables are presented in volume units (m^3 ha^{-1}), whereas the publications analyzed mainly employ mass units (dry mass). The results of yield-tables were presented in volume units (m^3 ha^{-1}) for two reasons. First, the results of yield-tables were not compared to results from separate study articles in the manuscript. Second, no separate data on grey alder wood density in individual countries were available for the conversion of volume units into mass units. Converting the volume units obtained from yield-tables with calculated mean wood density values from the regions described (from Scandinavia to Belarus) would have distorted the graphs of yield-tables (total volume and MAI) substantially and presenting these in an objective way would have been a dubious matter. For a better understanding, some wood density values for grey alder are given in Table 1. According to Wiemann and Williamson [57], the mean wood specific gravity of angiosperms gradually increases with decreasing latitude. Average wood densities reported from Nordic countries (Finland, Norway, Sweden) are lower than those reported from countries located further south (Latvia) (Table 1), which is most probably related to a higher mean annual temperature and a longer vegetation period.

Owing to different interpretations of data and highly diverse experimental designs, the summarizing and representation of data was rather complicated. Both natural and cultivated stands have been studied; different fertilization treatments and thinning operations have been applied; stand growth data have been reported from mineral soils (both

Table 1 – Grey alder wood densities in different countries.

Country	Density kg m^{-3}	Source
Norway	365	[45]
Sweden	359	[78]
Finland	361 353	[74,75] [68]
Estonia	396	[76]
Latvia	420	[77]

former arable land and forest land) and peat soils. Data on sample areas obtained from publications have been added to Table 3 (soil, treatment, density, biomass, location, etc.), to give as precise of a reflection as possible of the areas studied. Due to the data that was summed up, the table gives an opportunity to review the results published in this field and make comparisons between research papers more easily.

3. Results and discussion

3.1. Yield-tables

The majority of yield-tables presented in this study were compiled quite a long time ago and, due to several factors (drainage, CO_2 level increase in the atmosphere, etc.) they may not reflect the present situation. For example, during the previous half-century, the growth and productivity of Estonian forests have increased [58]. At the same time, the existing yield-tables are only appropriate for describing general growth dynamics and for comparing the growth patterns of different regions. Moreover, no recent grey alder yield-tables have been compiled, as the economic importance of the species is considered low in forestry.

3.1.1. *Mean annual increment*

The mean annual increment (MAI) shows the productivity of stand. The purpose of the SRF stand is to produce a maximum amount of biomass in the shortest possible time. In order to harvest a maximum yield of biomass and to manage the SRF stand most efficiently, it should be cut after the decline of MAI. Thus, MAI is an essential indicator for estimating effective rotation age. In the reported yield-tables, MAI reaches its peak at the age of 15…20 years in four cases out of seven (Fig. 1, Table 2). In regions that are located further south and have a warmer climate (Lithuania, Belarus), MAI peaks even earlier.

According to the data from yield-tables, grey alder stands in Belarus should already be harvested after 10 years of growth – this due to the abrupt decrease in MAI causing low accumulation of the standing volume. A rapid decrease in MAI after the age of 15 years can be noted in the tables from Latvia (Ozolz, Murnieks). In the tables from Lithuania (Jankauskas) and Estonia (Raukas), the decline is rather gradual (Fig. 1). In Finland and Norway, the growth dynamics of grey alder stands is similar: the increase in MAI values is relatively steady, peaking at the age of 30…35 years (Table 2); however, the absolute values of MAI are much higher in Norway. In these countries (Nordic region), a longer rotation period (30…35 years) is more suitable As is evident from Fig. 1, the most preferable cutting age for grey alder stands starts after

Table 2 – Values of MAI (stem volume DM m^3 ha^{-1}), stem volume (m^3 ha^{-1}) and number of trees per hectare on the basis of different yield tables.

Age	Jankauskas (LIT)	Yurkevich (BLR)	Murnieks (LAT)	Raukas (EST)	Børset & Langhammer (NOR)	Ozols & Hibners (LAT)	Miettinen (FIN)
5	10.0	7.6	7.8				
	50	38	39				
	15 745	28 400	15 916				
10	10.2	10.2	10.6	9.8		11.0	5.7
	102	102	106	98		110	57
	4443	5890	6004	14 000		12 000	31 000
15	10.2	9.7	11.4	10.3	9.7	11.3	6.5
	153	145	171	155	145	170	98
	2653	2720	3323	12 000	6100	6500	14 000
20	9.8	9.1	11.3	10.2	11.2	9.8	7.1
	196	182	226	204	224	194	142
	2023	1910	2348	8000	4500	4400	9500
25	9.4	8.5	10.8	9.7	11.9	8.8	7.4
	235	212	270	243	297	220	185
	1685	1530	1826	4000	3300	4000	6500
30	8.9	7.9	10.2	9.0	12.1	8.2	7.6
	268	238	307	270	363	246	228
	1490	1290	1497	2000	2500	3600	5000
35	8.5	7.3	9.5	7.9	12.0	7.9	7.7
	296	256	334	277	420	273	270
	1382	1170	1309	–	2100	2700	3500
40	8.0	6.7	8.9		11.7	7.6	
	319	269	354		468	300	
	1302	1100	1183		–	1800	
45	7.4	6.2	8.1				
	335	280	366				
	1242	1060	1089				
50	7.0	5.7	7.5				
	349	286	373				
	1205	1030	1035				

Table 3 – Data of grey alder stands reported in literature.

Source	Age, y	Location	Provenance	Nat. stand/ Plantatation	Treatment	Soil	Initial density trees ha^{-1}	Stand density trees ha^{-1}	Fertilization	Branches /Leaves	BM t ha^{-1}	Stem mass t ha^{-1}	MAI (stem) t ha^{-1}	CAI (stem) t ha^{-1}	Remarks
[17]	5			Nat.		M[a]							3.4	17	
[21]	2	Southern-Estonia 58°3′ N 27°12′ E		Plant	None	*Planosol*	15,750	15,750		B + L[b]	0.4	0.1	0.1	0.1	
[21]	3	Southern-Estonia 58°3′ N 27°12′ E		Plant.	None	*Planosol*	15,750	14,020		B + L	2.7	1.7	0.6	1.7	
[21]	4	Southern-Estonia 58°3′ N 27°12′ E		Plant.	None	*Planosol*	15,750	13,110		B + L	7.6	4.9	1.2	3.2	
[21]	5	Southern-Estonia 58°3′ N 27°12′ E		Plant.	None	*Planosol*	15,750	12,660		B + L	12.3	8.2	1.6	3.3	
[21]	6	Southern-Estonia 58°3′ N 27°12′ E		Plant.	None	*Planosol*	15,750	11,910		B + L	15.9	11.9	2	3.8	
[27]	22	West Tofts, UK		Plant.	Thinned 13.8 t ha^{-1} boles removed	M, former agric.		1656		B + L	124.7	91.7	4.17		
[29]	14	Southern-Estonia		Nat		M, riparian stand		5240			93.1	81.7	5.8	8.3	Mixed stand, 86% alders
[29]	40	Southern-Estonia		Nat		M, riparian stand		1390	Heavily polluted with N and P		131.8	104.7	2.6	4.2	Mixed stand, 77% alders
[30]	6	Southern-Sweden 56°0′ N 13°0′ E	Vestskoven (Denmark)	Plant.	Weeded annually till canopy closure	*Cambisol*, former agric.	5000			Leafless	26.7				
[31]	10	Southern-Estonia 58°3′ N 27°12′ E		Plant.	None	*Planosol*	15,750	7400		B + L	49.4	41	4.1	6.4	
[32]	7	Southern-Estonia 58°3′ N 27°12′ E		Plant.	None	*Planosol*	15,750	9850		B + L	25.3	18.6	2.7	6.7	
[32]	8	Southern-Estonia 58°3′ N 27°12′ E		Plant.	None	*Planosol*	15,750	9350		B + L	35.4	26.8	3.4	8.2	
[32]	9	Southern-Estonia 58°3′ N 27°12′ E		Plant.	None	*Planosol*	15,750	8400		B + L	40.4	34.6	3.8	7.8	
[32]	12	Southern-Estonia 58°3′ N 27°12′ E		Plant.	None	*Planosol*	15,750	6780		B + L	68.8	57.7	5.2	8.4	

[49]	4	Southern-Finland 60°57′ N 74°31′ E	Plant.		Fine sand	40,000	38,000	N, P, K, Ca, Mg, Cu, Zn, Mn	B + L	17.0	11.7	2.9		The results are average values of four different fertilization treatment plots
[49]	6	Southern-Finland 60°57′ N 74°31′ E	Plant.		Fine sand	40,000	32,000	N, P, K, Ca, Mg, Cu, Zn, Mn	B + L	31.0	26	4.3		
[50]	6	Mid-Finland 64°06′ N 25°36′ E	Plant.	Limed before planting	Cut-away peatland	20,000		P, K, micro		24.1				
[50]	6	Mid-Finland 63°54′ N 27°29′ E	Plant.	Harrowed before planting	Clay -mineral	20 000		P, K, micro		7.2	3.3	0.6		
[51]	6	Southern-Estonia	Nat.		*Planosol*		19,900			50.9			14.8	
[53]	27	Mid-Sweden 60°17′ N 16°01′ E	Nat.		Silt		3000		B + L	54.3	48	1.78		
[53]	25	Mid-Sweden 60°35′ N 15°47′ E	Nat.		Silt		13,133		B + L	38.6	34.7	1.39		
[53]	35	Mid-Sweden 60°22′ N 15°36′ E	Nat.		Silt		10,958		B + L	80.0	71.4	2.04		
[53]	10	Mid-Sweden 60°51′ N 15°06′ E	Nat.		Fine sand		16,800		B + L	34.6	31.2	3.12		
[53]	7	Mid-Sweden 60°28′ N 14°25′ E	Nat.		Fine sand		22,500		B + L	22.1	20	2.86		
[53]	10	Mid-Sweden 60°27′ N 15°25′ E	Nat.		Fine sand		7400		B + L	98.6	87.4	8.74		
[53]	15	Mid-Sweden 60°27′ N 15°25′ E	Nat.		Fine sand		47,600		B + L	32.1	29.2	1.95		
[53]	15	Mid-Sweden 60°27′ N 15°25′ E	Nat.		Fine sand		8600		B + L	139.8	123.8	8.25		
[53]	15	Mid-Sweden 63°10′ N 17°13′ E	Nat.		Light clay		17,500		B + L	60.4	54.3	3.62		
[53]	15	Mid-Sweden 63°14′ N 17°12′ E	Nat.		Fine sand		16,800		B + L	132.2	117.9	7.86		
[53]	6	Mid-Sweden 63°14′ N 17°11′ E	Nat.		Fine sand		60,200		B + L	23.0	21	3.5		

(continued on next page)

Table 3 – (continued)

Source	Age, y	Location	Provenance	Nat. stand/ Plantatation	Treatment	Soil	Initial density trees ha^{-1}	Stand density trees ha^{-1}	Fertilization	Branches /Leaves	BM t ha^{-1}	Stem mass t ha^{-1}	MAI (stem) t ha^{-1}	CAI (stem) t ha^{-1}	Remarks
[53]	5	Mid-Sweden 63°10′ N 17°28′ E		Nat.		Fine sand		94,000		B + L	3.3	3	0.6		
[53]	14	Mid-Sweden 63°14′ N 17°14′ E		Nat.		Fine sand		14,800		B + L	108.1	96.4	6.89		
[53]	8	Mid-Sweden 63°10′ N 17°35′ E		Nat.		Silt		65,000		B + L	24.9	22.7	2.84		
[53]	17	Mid-Sweden 62°58′ N 17°45′ E		Nat.		Fine sand		17,500		B + L	63.6	57	3.35		
[54]	10	Mid-Sweden 60°10′ N 16°7′ E		Nat.		M		5000		Stems		150			
[54]	35	Mid-Sweden 60°23′ N 16°6′ E		Nat.		M		1600		Stems		360			
[54]	1	Mid-Sweden 60°10′ N 16°7′ E		Nat. regen. from stumps and roots	After clear-cut	M		187,000		Stumpshoots + rootsuckers		1.1	1.1	1.1	
[54]	2	Mid-Sweden 60°10′ N 16°7′ E		Nat. regen. from stumps and roots	After clear-cut	M		148,000		Stumpshoots + rootsuckers		6.1	3.1	5	
[54]	3	Mid-Sweden 60°10′ N 16°7′ E		Nat. regen. from stumps and roots	After clear-cut	M		107,000		Stumpshoots + rootsuckers		10.9	5.4	4.7	
[54]	1	Mid-Sweden 60°23′ N 16°6′ E		Nat. regen. from stumps and roots	After clear-cut	M		188,000		Stumpshoots + rootsuckers		0.9	0.9	0.9	
[54]	2	Mid-Sweden 60°23′ N 16°6′ E		Nat. regen. from stumps and roots	After clear-cut	M		230,000		Stumpshoots + rootsuckers		7.3	3.7	6.4	
[54]	3	Mid-Sweden 60°23′ N 16°6′ E		Nat. regen. from stumps and roots	After clear-cut	M		115,000		Stumpshoots + rootsuckers		13.7	6.9	6.4	
[33]	40 ± 2 range 21–66	Northern- and Middle-Sweden 58°20′ –63°29′ N and 13°21′ –17° 35′ E		Nat.	Most stands thinned	25- Mineral; 1-Peat		1854 ± 213 range 546–4031		B + L	138.6 ± 7.2 range 82.2–218.4	112.0 ± 0.9 range 66.0 –223.9	3.44 ± 0.21 range 2.07–5.51		

[56]	43	Sweden						2005			133.0		3.1		
[65]	13	East-Central Sweden 60°49′ N 16°30′ E	Siljansfors	Plant.	Thinned twice	Drained sphagnum bog	40,000	6400	N, P, K, Ca, Mg, S				4.7	8.2	Plants raised in pots,
[65]	13	East-Central Sweden 60°49′ N 16°30′ E	Siljansfors	Plant.	No thinning	Drained sphagnum bog	40,000	22,500	N, P, K, Ca, Mg, S				4.4	10.9	inoculated with *Frankia*
[66]	3	Central-Sweden 69°49′ N 16°30′ E	Loppi R1-77-E3899	Plant.	Irrigation, weed control	Nutrient poor sandy soil	20,000		Annualy N, K, P, Ca, Mg		1.9				Before planting inoculated
[66]	4	Central-Sweden 69°49′ N 16°30′ E	Loppi R1-77-E3899	Plant.	Irrigation, weed control	Nutrient poor sandy soil	20,000		Annualy N, K, P, Ca, Mg		3.9			2.1	with *Frankia*
[66]	5	Central-Sweden 69°49′ N 16°30′ E	Loppi R1-77-E3899	Plant.	Irrigation, weed control	Nutrient poor andy soil	20,000		Annualy N, K, P, Ca, Mg		10.0			6	
[67]	5	Alaska, Tanana River floodplain		Nat.		Fertile river floodplain (sand)		50,000 (alders)		B + L	8.8	5.4	1.1		Mix with willow 50/50
[67]	15	Alaska, Tanana River floodplain		Nat.		Fertile river floodplain (sand)		4500		B + L	27.8	20.2	1.3		
[64]	20	Alaska, Tanana River floodplain		Nat.		Fertile river floodplain (sand)		7100		B + L	42.7	31.4	1.6		
[65]	6	Central-Finland		Nat.		Mineral		51,200		Leafless	20.1	16.7	2.6		
[65]	8	Central-Finland		Nat.		Mineral		39,300		Leafless	34.5	28.6	3.6		
[69]	10	Southern-Estonia		Nat.		Mineral, *Aegipodium*		15,900			65.1	59.7	6	8	
[70]	24	Central-Norway 64°30′ N 12°00′ E						4860			121.7	120.7	5		
[70]	40	Central-Norway 63°47′ N 11°40′ E						2050			133.2	110.2	3.3		
[71]	26	Central-Norway 63°47′ N 11°40′ E						1940				62.8	2.4		
[71]	41	Central-Norway						1800			124.6		3.1		

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Table 3 – (*continued*)

Source	Age, y	Location	Provenance	Nat. stand/ Plantatation	Treatment	Soil	Initial density trees ha^{-1}	Stand density trees ha^{-1}	Fertilization	Branches /Leaves	BM t ha^{-1}	Stem mass t ha^{-1}	MAI (stem) t ha^{-1}	CAI (stem) t ha^{-1}	Remarks
[60]	6	Central-Finland 64°06′ N 25°36′ E		Plant.	Limed and harrowed before planting. Weed contr. 3 years	Cut-away peatland	20,000	13,200	P,K, micro biannually	Leafless			4		Nodules were added to peat during planting
[60]	11	Central-Finland 64°06′ N 25°36′ E		Plant.	Limed and harrowed before planting. Weed contr. 3 years	Cut-away peatland	20,000		P,K, micro biannually	Leafless			4.7		
[60]	19	Central-Finland 64°06′ N 25°36′ E		Plant.	Limed and harrowed before planting. Weed contr. 3 years	Cut-away peatland	20,000	4400	P,K, micro biannually	Leafless	85		4.5		
[51]	5	Southern-Finland 61°50′ N 25°52′ E		Sprouting	Stemwood harvesting	Mineral. *Oxalis-Myrtillus*				B + L	13.5	9.7	2		
[39]	5	Southern-Finland 61°50′ N 25°52′ E		Sprouting	Whole-tree harvesting	Mineral. *Oxalis-Myrtillus*				B + L	8.3	4.9	1		
[39]	5	Southern-Finland 61°50′ N 25°52′ E		Sprouting	Whole-tree harvesting	Mineral. *Oxalis-Myrtillus*			Wood ash, P, K, micro	B + L	20.4	13	2.6		
[39]	5	Southern-Finland 61°50′ N 25°52′ E		Sprouting	Whole-tree harvesting	Mineral. *Oxalis-Myrtillus*			Wood ash, P, K, micro	B + L	21.4	13.6	2.7		
[39]	8	Southern-Finland 61°50′ N 25°52′ E		Sprouting	Stemwood harvesting	Mineral. *Oxalis-Myrtillus*				B + L	24.4	19.2	2.4		

[39]	8	Southern-Finland 61°50′ N 25°52′ E	Sprouting	Whole-tree harvesting	Mineral. *Oxalis-Myrtillus*				B + L	15.7	12.2	1.5		
[39]	8	Southern-Finland 61°50′ N 25°52′ E	Sprouting	Whole-tree harvesting	Mineral. *Oxalis-Myrtillus*			Wood ash, P, K, micro	B + L	29.5	23.1	2.9		
[39]	8	Southern-Finland 61°50′ N 25°52′ E	Sprouting	Whole-tree harvesting	Mineral. *Oxalis-Myrtillus*			Wood ash, P, K, micro	B + L	34.3	26.5	3.3		
[72]	5	Southern-Finland 61°11′ N 25°07′ E	Plantation	Harrowing before planting, weed control	M, former agric., fine sand		7700	Wood ash	B + L	9	4.7	0.9		Planted 5-month-old saplings, cultivated in pots
[72]	5	Southern-Finland 61°11′ N 25°07′ E	Plant.	Harrowing before planting, weed control	M, former agric., fine sand	10,000	6800	Wood ash, superphosphate, PK, micro	B + L	7.7	3.6	0.7		
[72]	5	Southern-Finland 61°11′ N 25°07′ E	Plant.	Harrowing before planting, weed control	M, former agric., fine sand	10,000	6800	Wood ash, ammonium nitrate, lime	B + L	4.4	1.9	0.4		
[72]	9	Southern-Finland 61°11′ N 25°07′ E	Plant.	Harrowing before planting, weed control	M, former agric., fine sand	10,000	6300	Wood ash	B + L	25.1	16.9	1.9		
[72]	9	Southern-Finland 61°11′ N 25°07′ E	Plant.	Harrowing before planting, weed control	M, former agric., fine sand	10,000	6000	Wood ash, superphosphate, PK, micro	B + L	24.2	16.3	1.8		
[72]	9	Southern-Finland 61°11′ N 25°07′ E	Plant.	Harrowing before planting, weed control	M, former agric., fine sand	10,000	6000	Wood ash, ammonium nitrate, lime	B + L	18.5	11.5	1.3		
[73]	3	Western-Russia, Yaroslavl oblast 57° N 39° E	Nat.		M, former agric.		156,000		B + L	24.5	17.2	3.4		
[73]	5	Western-Russia, Yaroslavl oblast 57° N 39° E	Nat.		M, former agric.		96,200		B + L	13.5	9.9	2	1.8	

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Table 3 – (*continued*)

Source	Age, y	Location	Provenance	Nat. stand/ Plantatation	Treatment	Soil	Initial density trees ha^{-1}	Stand density trees ha^{-1}	Fertilization	Branches /Leaves	BM t ha^{-1}	Stem mass t ha^{-1}	MAI (stem) t ha^{-1}	CAI (stem) t ha^{-1}	Remarks
[73]	18	Western-Russia, Yaroslavl oblast 57° N 39° E		Nat.		M, former agric.		8100		B + L	72.3	63.3	3.5	6.7	
[73]	27	Western-Russia, Yaroslavl oblast 57° N 39° E		Nat.		M, former agric.		2300		B + L	131.7	115.1	4.3	7.6	
[73]	36	Western-Russia, Yaroslavl oblast 57° N 39° E		Nat.		M, former agric.		1700		B + L	99.2	91.3	2.5	4.9	
[73]	50	Western-Russia, Yaroslavl oblast 57° N 39° E		Nat.		M, former agric.		1600		B + L	138.7	120.4	2.4	3.4	
[73]	11	Western-Russia, Yaroslavl oblast 57° N 39° E		Nat.		Mineral, *Oxalis*		16,500		B + L	48.4	42.6	3.9	6.8	
[73]	25	Western-Russia, Yaroslavl oblast 57° N 39° E		Nat.		Mineral, *Oxalis*		225		B + L	56.7	46.6	3.6	5	
[73]	17	Western-Russia, Yaroslavl oblast 57° N 39° E		Nat.		Mineral, *Oxalis*		5000		B + L	70.4	64	3.8	7	
[73]	27	Western-Russia, Yaroslavl oblast 57° N 39° E		Nat.		Mineral, *Oxalis*		2100		B + L	77.1	59.5	2.2	5.4	
[73]	3	Western-Russia, Yaroslavl oblast 57° N 39° E		Nat.	Scarified	M, former agric.		524,000		B + L	6.6	3.3	1.1		
[73]	7	Western-Russia, Yaroslavl oblast 57° N 39° E		Nat.	Scarified	M, former agric.		24,000		B + L	24.8	19.2	2.7	3.7	
[73]	8	Western-Russia, Yaroslavl oblast 57° N 39° E		Nat.	Scarified	M, former agric.		18,300		B + L	33.9	27.8	3.5	4.7	

a M – mineral soil.
b B + L – biomass with branches and leaves.

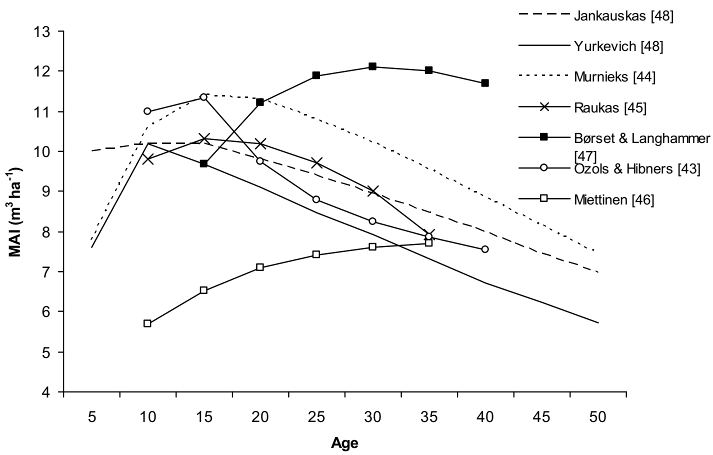

Fig. 1 – MAI values of grey alder stands on the basis of different yield tables. Values are given in dry matter.

the age of 15, with the exception of Norway and Finland. However, when the silvicultural purpose is to produce raw material for timber industry, other criteria should be applied with higher cutting age.

3.1.2. *Growing stock*

According to yield-tables, the stem volume increases for trees of up to 50 years of age in three cases (Table 2); the predicted accumulation of stem mass at the age of 50 remains under 400 m^3 ha^{-1}. Five yield-tables predict the growth of alder stands up to the age of 35...40. At the age of 35, the standing volume of grey alder stands in Latvia (Ozols & Hibners), Estonia and Finland measures up to ca. 280 m^3 ha^{-1}. In Norway, the stock is very high, amounting to almost 470 m^3 ha^{-1} at the age of 40. Evidently, from the view of practicality, it is not justified to let the stand grow up to such an old age, this because of the low increment of the growing stock and the higher risk of fungal infection in the late stages of stand upgrowth. At the age of 30...40 years, the spread of the heart rot *Phellinus igniarius* intensifies and may pass on to the next generation of vegetative regeneration [51].

According to the yield-tables, the predicted growing stocks range from 98 m^3 ha^{-1} to 171 m^3 ha^{-1} and from 142 m^3 ha^{-1} to 226 m^3 ha^{-1} at the ages of 15 and 20 years, respectively. Both higher and lower values are presented in the tables by Miettinen and Murnieks, respectively. The stem volume increment in the Børset and Langhammer (Norway) yield-table is low in younger tree age but is already among the highest, compared to the other tables, at the age of 20 (Fig. 2). At the age of bulk maturity (30...35), the accumulated growing stock is very high

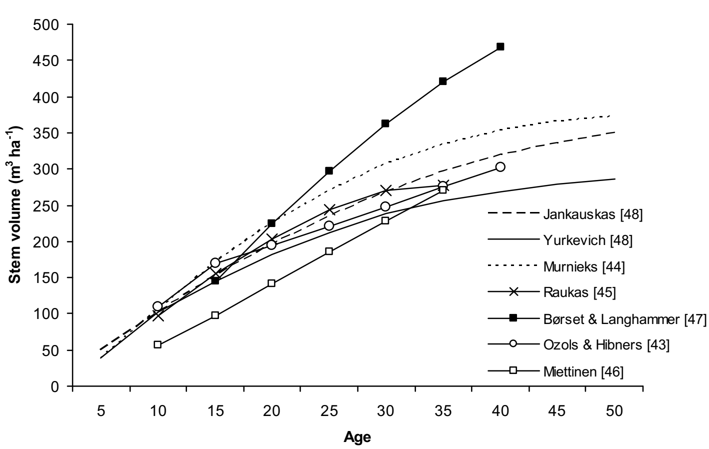

Fig. 2 – Stem volume dynamics of grey alder stands on the basis of yield tables. Values are given in dry matter.

in Norway. In Finland, the stem volume increment is low but stable. However, at the age of 35, the growing stock is appreciable. Compared to areas further in south, it takes a longer period of time to gain the same amount of production in Nordic regions.

At the age of 40…50 years, the stem masses in the yield-tables by Jankauskas and Murnieks exceed the corresponding masses in the other tables. Clear-felling at the age of 40…50 years in stands with a low incidence of stem injuries is most profitable if good timber quality is a priority [52]. Management of grey alder stand with a rotation period of 40…50 years is associated with the risk of economic loss (growth decrease, fungal diseases, stem rot).

3.1.3. *Stand density*

For natural grey alder stands, high density is inherent. According to the yield-tables, the number of trees per hectare in young stands (5-year-old) can almost amount to 30,000 (Table 2). At the early stage of stand development, rapid density decrease is evident (Murnieks, Ozols, Yurkevich). Fast differentiation of trees and self-thinning are typical for young grey alder stands (Table 2, Fig. 3). Only the data of the Finnish yield-table is an exception in this respect: in a 10-year-old stand, the number of trees is still rather high, namely 31,000. It is a well-known fact that growth intensity and stand self-thinning are positively correlated and forest growth and stand development are slower in Nordic regions due to the climate conditions.

From the economic aspect, initial stand density is one of the key issues when establishing a grey alder plantation for biomass production, as it affects the cost of stand establishment. In several grey alder experimental plantations, the applied high initial density ranged between 15,000 ha^{-1} to 40,000 ha^{-1} [21,49,50,59,60]. Optimal initial planting density can be deduced from the number of trees at the age of stand harvest. Due to the high frost hardiness, vitality and rapid growth of young alder trees, the mortality of young alder trees may be low. In the study by Uri *et al.* [21] the survival rate of the planted trees after one growing season was 94% despite the competition provided by herbaceous plants. Rapid decrease in the number of trees is noticeable in case of high initial density (Murnieks, Ozols, Yurkevich) (Table 2, Fig. 3). According to Table 2, mortality is very high during the stand age of 5…10 years. According to the table of Raukas, mortality accelerates after the age of 20 years. Opinions about the optimum density of SRF grey alder stand have been conflicting. Johansson [52] pointed out that in a dense stand growing at a fertile site, especially on former farmland, thinning should be done at a young age (<5 years) and the number of stems should not exceed 2000 ha^{-1}, especially if the stand is managed for timber production. The density suggested by Johansson seems to be too low for a 5-year-old short-rotation grey alder stand according to Uri *et al.* [32]. Biomass production per area unit depends largely on the number of stems and if stand density is too low, it may limit high biomass production. A report from Latvia recommends that thinning of young alder stands (age 3…5) should be done by decreasing the number of trees to 4000 ha^{-1} to 5000 ha^{-1} [61]. When comparing stand densities of the most productive yield-tables analyzed in the current paper, it is evident that at peak MAI, the densities of stands range from 2700 ha^{-1} to 6500 ha^{-1} at the age of 15. At the age of 20, the densities of the most productive yield-tables at that age range from 2400 ha^{-1} to 8000 ha^{-1}. The highest density occurs in the table of Estonia, while in all the other tables, density ranges from 2300 ha^{-1} to 4500 ha^{-1}. This estimation is in good accordance with the finding of Miežite [14], stating that at least 3000 ha^{-1} is the required density at the age of 14…17 years for growing grey alder stands with a high growing stock, which can be utilized for wood chip production, in a short period of time.

Consequently, according to the values presented in yield-tables, the optimal stand density of grey alder SRF stand

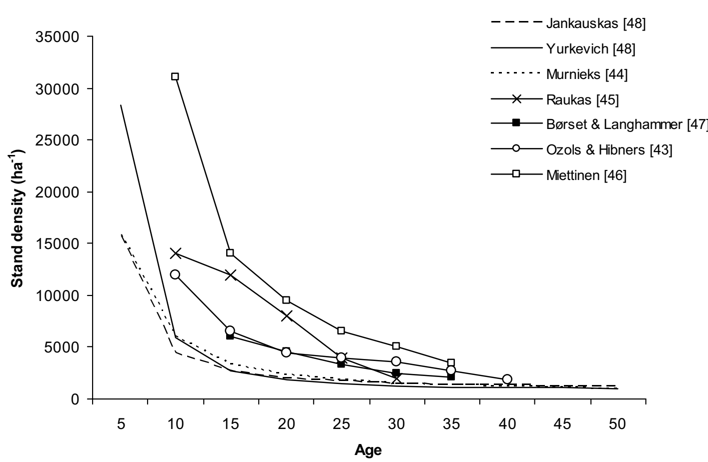

Fig. 3 – The dynamics of stand densities on the basis of different yield tables.

reaching bulk maturity should be in the range of 2500 ha^{-1}–6500 ha^{-1}. In the case of natural stand, owing to the absence of establishment costs, initial density is not of the greatest importance. Very few data are available about silvicultural treatment (e.g. thinning) of grey alder stand. According to Rytter [59], thinning of stands is not necessary in the case of high density: the results of a thinning experiment showed that about the same amount of obtainable biomass was produced in both thinned and unthinned control plots. Moreover, the size of trees removed during pre-commercial thinning is probably insufficient and their transportation and utilization may not be economically reasonable. Thinned stands with thicker but less numerous stems offer an advantage when the purpose of stand management is to produce timber. The thinning decision should be made individually for each stand, considering the (initial) density of the stand. A recommendation about the optimal density of SRF stand at the time of final harvesting is given above. In addition, what is essential is the age of the stand when thinned, since in the case of delay, the remaining trees do not respond to promoted growing conditions and cannot occupy the available growing space [59,62]. The results presented in Table 3 show that a stand density that is too high can be an obstructive factor for grey alder stand. The initial planting density of SRF grey alder plantation should most probably be lower than 10 000 ha^{-1}.

3.2. *Overview of published empirical data*

Table 3 presents the results from academic sources. It is clearly evident that the productivity of stand strongly depends on density. However, when comparing stands of the same age, it is often obvious that biomass accumulation and the mean annual increment are lower at extremely high than at lower stand densities. Productivity is not only dependent on stand density but also on soil and climate conditions.

Table 3 provides some notable values, both high and low. Rytter *et al.* [54] found a very high density of a juvenile stand regenerated from stumps after a clear-cut. Remarkable results regarding current annual increment (CAI), 17.3 t ha^{-1} and 14.8 t ha^{-1}, from stands of similar age were obtained by Granhall & Verwijst [1] and Tullus *et al.* [51], respectively. These results are the highest of their kind reported in the literature. A stem mass of 51 t ha^{-1} at the age of 6 years in the same experiment was reported by Tullus *et al.* [51]. A particularly high stem mass was found by Johansson [53] in a 15-year-old stand (123.8 t ha^{-1}). Some reported densities have also been remarkable. Johansson [53] reported high densities (47,600 and 13,000) in 15-year-old and 25-year-old stands, both with markedly low stem masses for their age, 29 t ha^{-1} and 35 t ha^{-1}, respectively.

However, grey alder is one of the possible tree species for SRF. In literature, many results about the biomass production of other potential tree species for SRF are reported. In Estonia, Tullus *et al.* [34] reported the results of 7-year-old hybrid aspen plantations growing on former agricultural lands. The results of leafless above-ground biomass averaged from 5.17 t ha^{-1}, range 2.18 t ha^{-1}–8.54 t ha^{-1}. Rytter and Sterner [35] reported the results for the hybrid aspen biomass production from Southern Sweden, where the total average of woody biomass production, including branches, of over 8 t ha^{-1} y^{-1} in young stands was obtained. Similar results about the silver birch indicate a large-scale variation of above-ground biomass production of the stands. Biomass production of five 8-year-old stands of silver birch growing on different soil types was reported in the study on abandoned agricultural land by Uri *et al.* [36]. The density of the stands studied varied from 3060 ha^{-1} to 36,200 ha^{-1} and their above-ground biomass varied from 6.0 t ha^{-1} to 22.9 t ha^{-1}. On a cut-away peatland in Central Finland, 19-year-old fertilized downy birch and silver birch plantations produced 112 t ha^{-1} and 108 t ha^{-1} leafless biomass, respectively, reported by Hytönen and Saarsalmi [60]. The biomass production and mean annual increment of 21- to 91-year-old common alder plantations on former agricultural land in Sweden ranged from 72.6 t ha^{-1} to 256.9 t ha^{-1} and 1.48 t ha^{-1}–6.06 t ha^{-1}, respectively [33]. In Estonia, the above-ground biomass of 21-year-old common alder plantations on fertile soil, which was formerly arable land, ranged from 80.2 t ha^{-1} to 94.0 t ha^{-1} [37].

The issue of optimal rotation age is crucial in forestry and has been addressed by many authors. The optimum of a rotation length of 15–20 years is supported by several studies [29,32,45,51,54,55,59,61,63,68]. All these results are in good accordance with the results of the optimum rotation period obtained from the yield-tables analyzed. Among the sources quoted, stands growing on different soils (also peat) and with different treatments (fertilized, thinned) have been represented. Both natural and planted stands can be found among them. Thus it seems that the question of rotation length is not about the different managements of stands; instead, it comes to absolute values. The decline of MAI seems to be species-specific and may not be so much dependent on soil conditions, stand treatment, etc., i.e. the volume gained during the rotation period in northern latitudes is probably remarkably lower than the respective value in areas located further south, as seen from yield-tables. However, at the age of 15–20 years, the stand increment is likely to start decreasing in alder stands located neither in Finland nor Latvia. Of course, there are other suggestions as well. Some studies have suggested a rotation length of up to 10 years [52,64]. Nevertheless, compared to the approach previously described, these viewpoints are outnumbered in the articles published.

Managing grey alder stands with a longer rotation length for sawtimber production purposes is an area that is studied very little by alder researchers. Hardly any management suggestions can be found. Still, Johansson describes one possible way of managing grey alder with a longer rotation. A rotation length of 40–50 years is recommended if good timber quality is a priority. Additionally, hard late thinnings and heavy clay soil sites should be avoided. For timber production, a dense stand on a fertile site and hard early thinning (age <5 years; number of stems after thinning <2000 ha^{-1}) should be suitable [52].

Precommercial thinnings as a management method for gaining saw logs from the stands have essentially been out of the researchers' focus. Rytter [59] discussed the effect of thinnings on the biomass production in dense plantations on peat bogs. The amount produced in unthinned areas exceeded the respective value of thinned areas. However, from the aspect of saw log production, the cost of thinnings must be compensated by the value of final harvesting.

Managing grey alder stands for saw log production with a rotation of up to 50 years may be problematic. The issues of the natural mortality of trees and diseases in mature grey alder stands must be considered when managing alder stands with such a long period of rotation. Apart from that, Fig. 2 shows that the wood volume increment at the stand age of 35–40 years is modest and postponing the clear-cut is economically unjustified.

The CAI is an indicator of the productivity potential of the site. In the case of favourable growth conditions, a high amount of biomass may be produced by grey alder stand. However, it is quite questionable to determine rotation length from the peak of CAI as this indicator fluctuates significantly from year to year depending on weather conditions [32,59]. Unfortunately, CAI has been reported in very few cases, probably due to its labour-intensive calculations.

4. Conclusion

The potential production capacity of grey alder stands in the Nordic and Baltic countries is high. A rapid growth in juvenile age, a high productivity capability, a symbiotic nitrogen fixation capacity, wide natural distribution, frost hardiness and a small number of damaging pests – these characteristics make grey alder a suitable tree species for short-rotation forestry in Scandinavian and Baltic states. Several studies on the productivity, growth and yield of grey alder have been carried out mostly by Scandinavian and Baltic scientists. Reports are available on experiments conducted with different designs (plantation/natural stand; mineral/peat soil; thinned/unthinned stand; unfertilized/various fertilization treatments; stands of different ages; stands with widely ranging densities) have been reported. Different results have been obtained about the biomass production of grey alder stands growing at different sites and under various conditions. It has proven its capability for fast growth both on mineral soil and on peatland. According to the yield-tables analyzed in the current paper, countries in the Baltic region are the most favourable for growing grey alder. On the basis of literature data, the optimal initial density grey alder plantation established for woody biomass production should be under 10,000 ha^{-1}. However, for economic and ecological reasons, it should remain lower. The recommended optimal density before clear-cut is in the range of 3000 ha^{-1}–6000 ha^{-1}. The optimal length of the rotation period for grey alder SRF stand, according to several yield-tables and literature sources, is around 15–20 years. The estimated growing stocks according to the yield-tables analyzed range from 98 $m^3\ ha^{-1}$ to 171 $m^3\ ha^{-1}$ and from 142 $m^3\ ha^{-1}$ to 226 $m^3\ ha^{-1}$ at the ages of 15 years and 20 years, respectively. The most productive grey alder stands reported have been found in Latvia, Estonia and Norway.

Studies about grey alder stand management for sawtimber production purposes are very scanty; almost no practical management suggestions have been given by researchers. However, the rotation length for grey alder timber production stands may be around 40 years.

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Long-term effects on the nitrogen budget of a short-rotation grey alder (*Alnus incana* (L.) Moench) forest on abandoned agricultural land

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ABSTRACT

Short-rotation energy forestry is one of the potential ways for management of abandoned agricultural areas. It helps sequestrate carbon and mitigate human-induced climate changes. Owing to symbiotic dinitrogen (N_2) fixation by actinomycetes and the soil fertilizing capacity and fast biomass growth of grey alders, the latter can be suitable species for short-rotation forestry. In our study of a young grey alder stand (*Alnus incana* (L.) Moench) on abandoned arable land in Estonia we tested the following hypotheses: (1) afforestation of abandoned agricultural land by grey alder significantly affects the soil nitrogen (N) status already during the first rotation period; (2) input of symbiotic fixation covers an essential part of the plant annual N demand of the stand; (3) despite a considerable N input into the ecosystem of a young alder stand, there will occur no significant environmental hazards (N leaching or N_2O emissions). The first two hypotheses can be accepted: there was a significant increase in N and C content in the topsoil (from 0.11 to 0.14%, and from 1.4 to 1.7%, respectively), and N fixation (151.5 kg N ha^{-1} yr^{-1}) covered about 74% of the annual N demand of the stand. The third hypothesis met support as well: N_2O emissions (0.5 kg N ha^{-1} yr^{-1}) were low, while most of the annual gaseous N losses were in the form of N_2 (73.8 kg N ha^{-1} yr^{-1}). Annual average NO_3–N leaching was 15 kg N ha^{-1} yr^{-1} but the N that leached from topsoil accumulated in deeper soil layers. The soil acidifying effect of alders was clearly evident; during the 14-year period soil acidity increased 1.3 units in the upper 0–10 cm topsoil layer.

1. Introduction

Land use changes are one of the key factors of climate change (IPCC, 2007). Since 1850, about 35% of anthropogenic CO_2 emissions have resulted from altered land use (Foley et al., 2005). Owing to climate warming, both C sequestration (Schimel et al., 2001) and global terrestrial net primary production (Nemani et al., 2003) have increased. However, soil fertility limits C sequestration by forest ecosystems in a CO_2-enriched atmosphere (Oren et al., 2001; Heath et al., 2005). On the other hand, elevated atmospheric nitrogen (N) deposition makes a minor contribution to C sequestration in temperate forests (Nadelhoffer et al., 1999; Liu and Greaver, 2009). Thus, it is believed that fast growing energy crops and short-rotation forests can mitigate anthropogenic greenhouse gas (GHG) emissions (Foley et al., 2005; Bonan, 2008). The nearest goal in the European Union is to increase the share of the energy generated from renewable sources from 5% to 12% by 2010 (Kuiper et al., 1998; EU Commission, 1997). In 2007, renewable energy made up already 7.8% of gross inland consumption (Europe's energy. . ., 2010). Future land use scenarios for Europe foresee a significant increase in energy crop areas (Rounsevell et al., 2006). Accordingly, the investigation of tree species suitable for short-rotation energy forestry and different related problems has been intensified.

The most suitable areas for bioenergy production are abandoned agriculture lands, which cover globally 385–472 million ha (Campbell et al., 2008). Although the energy content of potential biomass grown on these abandoned lands accounts for <10% of the primary energy demand for most nations in North America and Europe, for some regions like Eastern and Northern Europe (Peterson and Aunap, 1998; Larsson and Nilsson, 2005) as well as for mountainous areas of Europe (MacDonald et al., 2000), this potential is significant. A considerable increase in the area of abandoned agricultural lands, due to changes in the political and economic situation, has occurred in Eastern Europe, including

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Estonia, during last decades (Mander and Palang, 1994). According to a recent estimation, about 300,000 ha of agricultural lands are abandoned in Estonia (Astover et al., 2006).

In the zone of temperate and boreal forests, abandoned agricultural areas are predominantly afforested with deciduous trees. Different alder species are among the most common trees in these secondary successions: their invading former arable lands and meadows has been reported from Sweden (Granhall and Verwijst, 1994), Finland (Saarsalmi, 1995), Russia (Shvidenko et al., 1997), Norway (Staaland et al., 1998), Estonia (Uri et al., 2009), Korea (Lee et al., 2002), France (Anthelem et al., 2001), Swiss Alps (Frelechoux et al., 2007), Latvia (Liepins et al., 2008), and other areas. As pioneer species alders are successfully used for restoration of mining areas (Helm and Carling, 1993; Kramer et al., 2000; Frouz et al., 2001; Lõhmus et al., 2006a).

The essential advantage of alders is the symbiotic N_2 fixation ability of the actinomycete *Frankia* (Benson, 1982). Red alders (*Alnus rubra* Bong.) are widely used for improvement of soil fertility and biomass production in mixed alder-conifer stands (Binkley et al., 1992; Hart et al., 1997; Rothe et al., 2002; Binkley, 2003). In addition to increasing soil N, C, and available P content, microbial biomass and activity, red alders significantly alter community-level microbial functions in mixed stands (Selmants et al., 2005). Most of N from decomposed red alder leaves has been incorporated into growing plants and the soil pool (Swanston and Myrold, 1997). Other alder species have been successfully used as a source of biological fertilizers in mixed stands with walnuts (*Juglans nigra* mixed with *Alnus glutinosa*; Bohanek and Groninger, 2005) and agricultural crops (alleys of *Alnus crispa* subsp. *sinuta* in between sweet corn (*Zea mays*) rows; Seiter and Horwath, 1999). Owing to enhanced microbial activity and tree growth in alder stands, carbon fluxes are somewhat larger there than in other temperate forests (Kutsch et al., 2005). In general, alder species have a favourable impact both on the diversity and activity of the microbial communities of the soil and the rhizosphere (Lõhmus et al., 2006b), which has also been reported in relation to increased soil phosphorus availability under alder species (Binkley, 1984; Giardina et al., 1995; Uri et al., 2002; Gökkaya et al., 2006).

Several studies demonstrate that grey alder (*Alnus incana* (L.) Moench) is a most promising fast-growing tree species for a short-rotation forestry in Estonia (Uri et al., 2002, 2003b, 2009). This species is highly productive both on mineral and organic soils (Granhall and Verwijst, 1994; Saarsalmi, 1995; Rytter, 1996; Telenius, 1999). Hence, grey alder as an actinorrhizal N_2-fixing tree species can be used effectively for biological fertilization of the soil with N (Granhall, 1994). Owing to its symbiotic nitrogen fixation capacity, grey alder is able to cover a large proportion of its annual nitrogen demand with nitrogen from the atmosphere and, compared with other short-rotation energy forest tree species the need for expensive nitrogen fertilization will be smaller or lacking altogether. Grey alder has also some essential silvicultural advantages, which makes it a promising species for short-rotation forestry. Grey alder seedlings withstand direct sunlight and frost; they have only a few pests and diseases (Granhall and Verwijst, 1994). After cutting, a new alder generation emerges both from root suckers and stump sprouts owing to which artificial reforestation of clearcuts is not needed. Rytter (1995) demonstrated that thinning of *A. incana* stands is not necessary as it does not increase the mean annual increment of stands. A comparative study by Johansson (2000) shows that mean annual total above-ground biomass in Swedish grey alder stands was about 64% higher than in common alder (*A. glutinosa*) stands.

However, owing to symbiotic N fixation, introduction of additional nitrogen in the alder forest ecosystem, and enhanced nitrification, the pH value in soils can decrease resulting in leaching of nitrate and base cations (Van Miegroet and Cole, 1984, 1985; Verburg et al., 2001). Leaching of nitrates from soils under alder stands has been reported in several studies (Binkley et al., 1992; Van Miegroet et al., 1992; Compton et al., 2003) and even a low alder cover in riparian zones has been found to be a source of elevated N exports (Cairns and Lajtha, 2005). In riparian buffer zones of agricultural landscapes, which receive a concentrated lateral inflow from adjacent intensively fertilized areas uphill, the decrease in N loading is significant. Nevertheless, the outflow is lower (13.2 kg N ha^{-1} yr^{-1}; Lõhmus et al., 2002; Mander et al., 2008) than that found in red alder stands (Binkley et al., 1992). Intensive denitrification in riparian zones transforms nitrates to dinitrogen (N_2) and nitrous oxide (N_2O), 51.7 and 0.5 kg N ha^{-1} yr^{-1}, respectively, as reported by Mander et al. (2008).

Replacement of set-aside agricultural field by forest brings about various changes at different levels of ecosystems, including N cycling. Land use type may have an essential effect on soil C and N content, quality of organic matter, microbial activity and mineralization of organic N (Compton et al., 1998).

Cultivation of temperate soils may reduce soil nitrogen about 8% from the initial value (Post and Mann, 1990), but changes in soil N level and processes occurring after agricultural abandonment are not well established and are likely to be highly site specific (Compton et al., 1998). The effect of trees on the soil N status depends essentially on the tree species forming a new forest ecosystem. In the case of alders, the respective effect on the nitrogen budget and the soil N status is particularly significant owing to their symbiotic N fixation ability (Binkley, 2005). How is N cycling affected during the transition of the ecosystem from field to forest and what kind of possible environmental risks may occur in this process, taking into account N input by symbiotic nitrogen fixation? Long-term investigations of N budget in alder forests are almost lacking. To our knowledge, there is only one long-term study dealing with an *Alnus japonica* stand on an abandoned rice field in Korea, which reports an increase in soil N concentration during the first 8 years and stabilization at a level of 1.8% during the following 42 years (Lee et al., 2002).

The working hypotheses of the present case study were: (1) afforestation of abandoned agricultural land by grey alder significantly affects the soil N status already during the first rotation period; (2) symbiotic fixation input covers an essential part of the plant annual N demand of the stand; (3) despite a considerable N input into the ecosystem of a young alder stand, there will occur no significant environmental risks (N leaching or N_2O emissions).

To test these hypotheses, the main objectives of our study were: (1) to compile an N budget for a young short-rotation grey alder stand growing on abandoned agricultural land and to assess the influence of alders on the soil N status (*i.e.*, the potential of N-related environmental hazards); (2) to estimate the flux of the symbiotic N fixation of this 10-year-old grey alder stand; (3) to analyse formation of a forest ecosystem and the dynamics of functioning of this young grey alder stand on abandoned agricultural land in relation to N cycling.

2. Materials and methods

2.1. Study area

A grey alder plantation (0.1 ha) was established on abandoned farmland in spring 1995, in the southeastern part of Estonia, 58°3′ N and 27°12′ E. According to the data of the closest meteorological station, mean annual temperature, amount of precipitation and length of the vegetation period are 6 °C, 653 mm and 191 days, respectively. The soil is classified as *Eutric Podzoluvisol* (according to the FAO classification). One-year-old transplants of natural origin

Table 1
Mean (±standard error) nitrogen concentrations (g kg^{-1}) in different biomass fractions in the 10-year-old stand.

Grey alder		
Above-ground part	Leaves	33.7 ± 1.6
	Current year shoots	15.8 ± 0.3
	Branches	7.9 ± 0.6
	Bark	11.8 ± 0.2
	Wood	2.7 ± 0.3
Below-ground	Stump	4.1 ± 0.3
	Coarse roots $d > 10$ mm	7.9 ± 0.7
	Coarse roots $5 < d \leq 10$ mm	9.1 ± 0.5
	Coarse roots $2 < d \leq 5$ mm	10.3 ± 0.2
	Fine roots $d < 2$ mm	12.5 ± 0.2
	Nodules	19.2 ± 0.3
Herbaceous plants		
Above-ground part		27.6 ± 1.5
Below-ground part		17.3 ± 0.8

were used for planting. Initial density was 15,750 trees per hectare. No weed control, fertilization or other treatment was employed. The establishment, survival and growth of the plantation has been described earlier (Uri et al., 2002, 2009).

2.2. Estimation of nitrogen accumulation and annual nitrogen demand of the stand

In the present study, the annual N demand is defined as the amount of N bound in plant biomass produced in the current year.

The concentrations of N were determined from different compartments of biomass in 2003 (Table 1). Both the pool and the annual demand of N in the biomass of the plants were calculated; the biomass or the annual increment of a compartment was multiplied by the respective N concentration. For the roots and nodules, ash content was determined to additionally check possible contamination of the roots with the soil, it was <10% in all cases.

Above-ground biomass and current annual production (CAP) were estimated annually in the period 1995–2003 at the end of August when the process of biomass formation was completed; dimension analysis (Bormann and Gordon, 1984) was used. Model trees (7) were fractioned as described in Uri et al. (2002, 2003b). Biomass estimation and biomass production of the stand is described in Uri et al. (2009).

Nitrogen use efficiency (NUE) (kg kg^{-1} yr^{-1}) was calculated by dividing the CAP of the above-ground part biomass of the stand by the annual N demand for above-ground production.

The below-ground biomass of the stand was estimated in October 2003 using two different methods: excavation of the root system of the model trees for estimation of the biomass of the stump and the coarse roots ($d \geq 2$ mm), and soil coring for estimation of the biomass of the fine roots ($d < 2$ mm) and the nodules. Both methods are described in detail in earlier publications (Uri et al., 2002, 2009).

Annual coarse root production was estimated on the basis of mean annual increment in the coarse root fractions ($d \geq 10$ mm; $5 \leq d < 10$ mm; $2 \leq d < 5$ mm; stump) during 1998–2003.

Soil cores were used to estimate the biomass of the nodules and the fine roots (Vogt and Persson, 1991; Uri et al., 2002, 2009). The soil core data were used for calculation of the biomass of the fine roots and the nodules per hectare.

Fine root production was estimated by the in-growth core technique. Altogether 150 in-growth cores ($d = 40$ mm, mesh size 6 mm) were inserted into the soil in five random transect groups all over the area, and into the topsoil to a depth of 30 cm in October 1999. Mesh bags were filled with root-free soil according to the genetical horizons of the soil. A total of 105 in-growth core samples (15 per sampling) were collected during the growing seasons of 2000–2002. Sampling was carried out in November 2000, and in June, August and November 2001–2002. The cores were divided into subsequent 5 cm depth layers. The methods used are described more thoroughly in Ostonen et al. (2005).

In the laboratory, alder roots in the samples were washed to remove soil particles and were separated into living and dead roots. Both the living and the dead roots were separated into two diameter classes: $d < 1$ mm and $1 \text{ mm} \leq d < 2$ mm. The dry mass of the root samples was determined after drying of fine root samples at 70 °C to constant mass to 0.001 g. The in-growth cores were processed at the Salla Research Station, Finnish Forest Research Institute (Helmisaari et al., 2007).

Total fine root production was calculated on the basis of in-growth core data and by balancing the biomass compartments of the living and dead roots according to Fairley and Alexander (1985). Root turnover rate (yr^{-1}) was calculated as annual root production (kg ha^{-1} yr^{-1}) divided by mean fine root biomass (kg ha^{-1}) from in-growth cores. Mean, minimum and maximum root biomasses were used to calculate fine root turnover rate (Eissenstat and Yanai, 1997). We used mean fine root biomass instead of minimum or maximum biomass to avoid large fluctuations during the vegetation period (Ostonen et al., 2005).

2.3. Estimation of understorey production

For estimation of the above-ground biomass of the ground vegetation, samples were taken at the end of June when biomass was at a maximum. The above-ground part of all herbaceous plants was collected from a 1 m^2 quadrat at 10 randomly chosen points over the whole plantation. The samples were dried at 70 °C to constant weight and weighed to 0.01 g. As the above-ground part of herbs is annual, annual production is equal to biomass.

The below-ground biomass of the understorey was estimated on the basis of soil cores. Ten soil cores were taken to a depth of 30 cm in the same 1 m^2 quadrats using a soil auger ($d = 108.6$ mm). All cores were divided into three subsequent 10 cm layers and the roots and rhizomes were washed out of each layer. The roots and rhizomes of herbaceous plants were separated under a microscope. The samples were dried at 70 °C to constant weight and weighed to 0.001 g. For the below-ground fraction of the understorey, turnover rate was assumed to be 1 year (Lõhmus et al., 2002).

2.4. Transformations

2.4.1. Annual net nitrogen mineralization

Net N mineralization (NNM) was estimated *in situ* in the upper 10 cm soil layer. The experiment was performed using the method with incubated polyethylene bags (Adams et al., 1989; Hart et al., 1994; Uri et al., 2003a, 2008), based on measurement of mineral N in an environment from which the impact of intact roots is excluded. The first samples (24) were incubated in the experimental area on May 2003. At each random point an intact soil core was taken from the upper 10 cm soil layer with a cylindrical soil auger ($d = 48$ mm) and sealed in a polyethylene bag incubated in the same hole without damaging soil structure. Simultaneously with the incubation of new samples, an adjacent initial sample was taken from beside the incubated sample each time. Both the incubated and the initial samples were gathered from composite samples by three and were transported to the laboratory on the same day. As a result of one sampling, 8 incubated composite samples and 8 initial composite samples were gathered. Sampling and incubation were performed with a monthly interval until the ground was frozen. In spring, samples were incubated immediately after melting of the soil (April).

Decomposition of leaf litter in the grey alder stand was very fast; by the beginning of the following summer leaf litter had disappeared and we assumed that the N accumulated in leaf litter incorporated in the NNM flux. Consequently, the N flux from leaf litter decomposition was not estimated separately but within NNM.

We presumed that the rate of net N mineralization in deeper soil layer was similar to the corresponding rate estimated during the first net N mineralization experiment (Uri et al., 2003a). A more detailed description of sampling, sample processing and calculation of NNM and net nitrification is presented in Uri et al. (2003a, 2008).

2.4.2. Retranslocation in trees and below-ground starting pool of herbs

Annual N retranslocation in alders was estimated using leaf mass and differences in N concentrations between the fresh leaves and leaf litter (Uri et al., 2002). Leaf litter was gathered with the use of 10 litter traps (collecting area 0.25 m^2 each) during 1998–2004. The share of branch litter was negligible. Litter was sampled once a fortnight (during leaf fall once a week).

To estimate the autumn retranslocation of N in the ground vegetation, N concentration in the below-ground part of herbaceous plants was determined at maximum biomass (in the end of June) and in October in 2003. The soil coring technique is described above. It was assumed that the amount of N accumulated in the below-ground part of the ground vegetation in autumn covers part of the N demand of the following year.

2.5. Leaching and gaseous nitrogen fluxes

Nitrogen leaching was estimated on the basis of plate lysimeters. In autumn 2002, 10 plate lysimeters (stainless steel; collecting area 627 cm^2) were randomly installed in the soil to a depth of 40 cm. Polyethylene tubes connected the lysimeters with water collectors (5000 ml polyethylene canisters disposed at a depth of 1 m). Water from the canisters was sampled, using a peristaltic vacuum pump, through a plastic pipe. Water was sampled monthly from October 2002 to November 2003.

For measurement of N_2O and N_2 fluxes, two emission methods, the “closed chamber” (“closed soil cover box”) method (Denmead and Raupach, 1993; Hutchinson and Livingston, 1993) and the helium–oxygen (He–O) method (Butterbach-Bahl et al., 1997; Scholefield et al., 1997; Mander et al., 2003; Teiter and Mander, 2005) were employed. The latter was used, particularly, for measurement of N_2 fluxes. Eight replicates of gas samplers (closed chambers; cover made of PVC, height 50 cm, diameter 50 cm, volume 65 l, sealed with a water-filled ring on soil surface, painted white to avoid heating during application) were randomly installed in the study plot. At the end of 1 h measuring time, gas samples were taken from the enclosures of the samplers using previously evacuated 100 ml gas bottles. Gas sampling was carried out six times according to the following time schedule: in July and December 2003, in April and May 2005, and in November and December 2006. To avoid trampling of sites, boardwalks were established between the samplers and soil/groundwater measurement plots. Trace gas concentration in collected air was determined using a gas chromatography system (electron capture detector and flame ionization detector; Loftfield et al., 1997) in the laboratory of the Institute of Landscape Matter Dynamics, Leibniz Centre for Agricultural Landscape and Land Use Research (ZALF), Müncheberg, Germany. Trace gas flux rates were calculated according to Hutchinson and Livingston (1993) from the linear change in trace gas concentration over time with a reference to the internal volume of the chamber and the soil area covered. Soil temperature was measured simultaneously.

Intact soil cores (diameter 6.8 cm, height 6 cm) for use with the He–O method were sampled from the topsoil (0–10 cm) at the nearby sites (10–20 cm) sites of the gas sampler (closed chamber) after gas sampling was completed. Soil samples were weighed, kept at low temperature (4 °C), and transported to the ZALF laboratory. At the laboratory, intact soil cores were placed in special gas-tight incubation vessels. In these vessels, N_2 was removed using three subsequent slight evacuation/flushing cycles with an artificial gas mixture (21.3% O_2, 78.6% He, 337 ppm CO_2, 374 ppb N_2O, 1882 ppb CH_4 and approximately 5 ppm N_2). This procedure was followed by the establishment of a new flow equilibrium by continuously flushing the vessel headspace with the artificial gas mixture at 10 ml per min for 12 h. For the start value, the concentration of N_2 in the continuous gas flow was measured. Measurement of gas concentrations in the incubation headspace (final value) occurred after closure of the incubation headspace for 1 h to accumulate the emission of N_2 and greenhouse gases. The final accumulation value minus the start value of the continuous flow served as the basis for calculation of emission rates (Augustin et al., 1998). The procedures used for determination of actual gas flux rates are described in Mander et al. (2003).

2.6. Nitrogen deposition and symbiotic fixation

Deposition in this region was estimated earlier (1994–1996) and published in Mander et al. (1997). Use was made of the method of polyethylene gutter samplers according to the Manual for Integrated Monitoring (ICP, 1998).

The flux of symbiotically fixed N_2 used in the production of alders was estimated by balancing the other fluxes of the N budget (Lõhmus et al., 2002). After estimating the annual N use by plants, leaching and gaseous emission, it was assumed that the budget deficit was covered by symbiotic N fixation.

2.7. Soil sampling and laboratory analysis

Soil was sampled from the studied stand annually in the period 1995–2008 in October when plant growth had ceased. Ten random points were marked over the area, and soil samples were taken adjacent to these points each year to a depth of 50 cm. Samples from the subsequent 0–10; 10–20; 20–30; 30–40 and 40–50 cm soil layers were gathered to form composite samples. Samples from 10 random points were gathered for three composite samples (the first composite sample from the first three points, the second from the three next points and the third from the last four points). In total, three composite samples from every soil depth layer were included in analysis each year. For testing the soil samples for N according to Kjeldahl, Tecator ASN 3313 was employed. The concentration of organic matter (%) was determined as loss on ignition at 360 °C (LOI). Total C concentrations (%) in the soil layers were determined with a CHN analyser (Perkin-Elmer 6400 Series II).

For calculation of N or C storage in the soil, soil bulk density was determined in 2002 when 10 lysemeters were installed in the stand. For this purpose, 10 soil pits (1.0 m deep) were dug. From every pit bulk density samples were taken from different soil layers (0–50 cm) with a stainless steel cylinder (d = 40 mm and volume 50.24 cm^3) avoiding compression of the soil. Three samples were taken from each layer. The samples were dried in laboratory at 105 °C and weighed.

Determination of available phosphorus in the soil was performed by flow injection analysis (ammonium lactate extractable) with the use of Tecator ASTN 9/84.

Plant samples were analysed for total N by the Kjeldahl method using a “Kjeltec Auto 1030” analyser. Determination of $NH_4{}^+$–N, $NO_2{}^-$–N, and $NO_3{}^-$–N in the lysimeter water was performed by

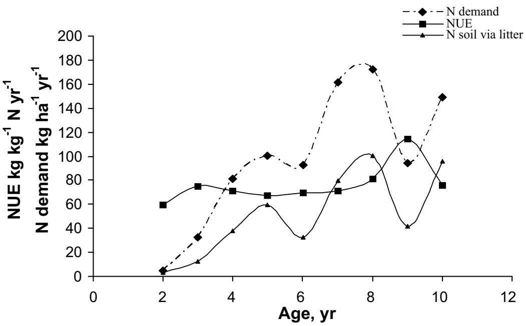

Fig. 1. The dynamics of nitrogen use efficiency (NUE), annual N demand and N flux in to soil via leaf litter in grey alder stand. All characteristics are calculated for the above-ground part of the stand.

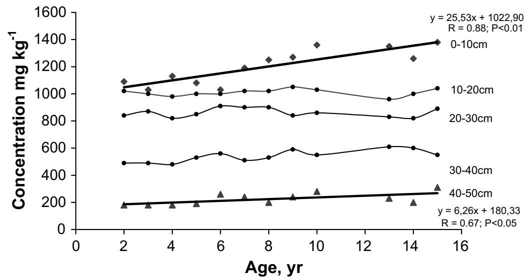

Fig. 2. The dynamics of soil nitrogen concentration in different soil layers of grey alder stand.

flow injection analysis with the use of Tecator ASN 65-32/84 and Tecator ASN 65-31/84, respectively.

Analyses were carried out at the Biochemistry Laboratory of the Estonian University of Life Sciences.

2.8. Statistical methods

Normality of variables was checked by Lilliefors and Shapiro–Wilk's tests. To analyse the effect of the qualitative factors on the response variables, two-way ANOVA was applied. ANOVA assumptions – normality, homogeneity of group variances and nonsignificant relationship between the group means and the standard deviations – were checked. The Tukey HSD test was used for multiple comparison of the means in case the assumptions were satisfied; the *t*-test was employed to compare means for the two groups.

When data did not follow a normal distribution, or when there occurred inhomogeneity of group variances the nonparametric Kruskal–Wallis analysis of variance was used. Linear and allometric models were employed for estimating the relationships. In all cases the level of significance $\alpha = 0.05$ was accepted. The software STATISTICA 7.0 was used (StatSoft Inc.)

3. Results

3.1. Annual N demand of plants

The amount of N used for the annual production of tree biomass in the above-ground part of the 10-year-old grey alder stand was 149 kg ha^{-1} yr^{-1}, while 70% (104 kg) of this was accumulated in the leaves (Table 2). Total N accumulation in the above-ground biomass of the trees amounted to 301 kg ha^{-1}. NUE was a highly stable characteristic (Fig. 1), a significant increase in NUE was noted in the drought year of 2002.

The mean annual increment of the biomass of the coarse root fractions in the 10-year-old stand was estimated as 1.35 t ha^{-1} yr^{-1} and annual N use was estimated as 9.2 kg ha^{-1} yr^{-1}. Total nitrogen accumulation in the coarse root fractions was 59.4 kg ha^{-1} yr^{-1}.

The within-site horizontal variability of fine root biomass was statistically nonsignificant (Kruskal–Wallis ANOVA, $P > 0.28$). There was no significant difference between fine root biomass values determined by soil cores and in-growth cores. The 95% confident limits for fine root biomass from in-growth cores were from 554 kg ha^{-1} to 1410 kg ha^{-1}, the value for soil cores remains within these limits. The mass of the fine roots ($d < 2$ mm) and incorporated N was 870 kg ha^{-1} and 10.9 kg ha^{-1}, respectively. The total fine root production and turnover rate were calculated as 530 kg ha^{-1} yr^{-1} and 0.54 yr^{-1}, respectively. The nitrogen demand for the annual fine root production was estimated at 6.6 kg ha^{-1} yr^{-1}. The mass of the nodules at stand ages 5 and 10 years was similar, 169 ± 78 kg ha^{-1} (Uri et al., 2002) and 156 ± 60 kg ha^{-1}, respectively. The total accumulation of N in the nodules was 3 kg ha^{-1}.

The above-ground biomass of the herbaceous vegetation of the understorey was 880 kg ha^{-1}, and N accumulation was 24.3 kg ha^{-1}. The biomass of the below-ground part of the understorey was 950 kg ha^{-1} and the N pool was 16.4 kg ha^{-1}. Hence, the total annual N demand of the herbaceous plants was 40.7 kg ha^{-1}.

3.2. Soil

In the experimental area, the total N pool in the upper 10 cm layer was 1.39 t ha^{-1} and in the 10–20 cm layer 1.31 t ha^{-1} at the establishment of plantation (1995). During 14 growing years (1995–2008) a significant flux of N reached the soil with leaf litter. The amount of N added to the soil by leaf litter in the 10-year-old stand was 95 kg ha^{-1} yr^{-1}.

The increase in soil Kjeldahl N during 14 years was statistically significant ($R = 0.88$; $P < 0.01$) in the upper 0–10 cm and deeper 40–50 cm ($R = 0.67$; $P < 0.05$) soil layers (Fig. 2). In the middle soil layers (10–40 cm) N concentration did not change significantly. The change of N concentration in the soil yielded an increase of 370 kg ha^{-1} in the 0–10 cm soil layer during 14 years after planting. In the deeper soil layer (40–50 cm), during the same period, the increase was 215 kg ha^{-1}.

After the afforestation of the agricultural land by alders, soil pH started to decrease. During 14 years soil acidity increased by 1.3 units in the upper 0–10 cm topsoil layer ($R = 0.90$; $P < 0.05$). A similar trend was also evident in the deeper soil layer (40–50 cm) (Fig. 3) where soil acidity increased by 1.0 unit ($R = 0.91$; $P < 0.05$).

The soil organic carbon (C) pool increased significantly ($R = 0.68$; $P < 0.05$) in the upper 0–10 cm soil layer (Fig. 4). Total C sequestration in the soil during 14 years after the establishment of the stand was 4.8 t ha^{-1} in the upper 0–10 cm soil layer. In the deeper soil layers, soil C content did not change.

3.3. Nitrogen fluxes

Annual net nitrogen mineralization (NNM) in the upper 0–10 cm soil layer and in the upper 10–20 cm soil layer was 74.1 kg ha^{-1} yr^{-1} and 49.9 kg ha^{-1} yr^{-1}, respectively. The share of net nitrification in total NNM was 100%.

Table 2
Fluxes (kg N ha^{-1} yr^{-1}) of the nitrogen budget in the 5-year-old (Uri et al., 2004) and in the 10-year-old grey alder stands on abandoned agricultural land.

Demand of plants		5-year-old 234.1[a]	10-year-old 205.2[a]
Trees	Above-ground part	108.1[a]	148.7[a]
	Leaves	77.6	104.4
	Stem	14.3	24.9
	Current year shoots	10.6	10.4
	Old branches	5.6	9.0
	Below-ground part	21.8[b]	15.8[a]
	Coarse roots and stump		9.2
	Fine roots (d < 2 mm)		6.6
	Nodules		n.e
Herbs	Above-ground part	64.3[a]	24.3[a]
	Below-ground part	39.9[a]	16.4[a]
Inputs			
Deposition		6.4[b]	6.4[b]
Symbiotic fixation		>41.7[c]	151.5[c]
Transformations			
Net nitrogen mineralization		141.2[a]	124.0[a]
Retranslocation from senescing leaves		4.4[a]	6.3[a]
Starting pool of herbaceous plants		19.5[a]	6.2[a]
Output			
Leaching		n.e.	14.9[a]
Gaseous losses		n.e.	74.3[a]

n.e. – not estimated.
[a] Determined.
[b] Estimated on the basis of literature data.
[c] Calculated by balancing other values.

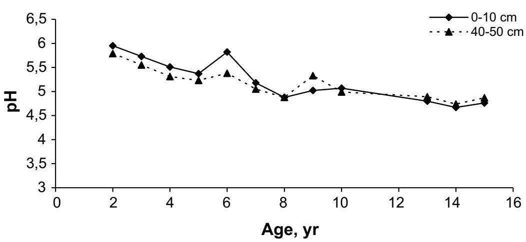

Fig. 3. The dynamics of soil pH in different depth layers in young grey alder stand. Bars indicate standard errors.

Nitrogen retranslocation from the senescing leaves of the grey alders was estimated at 6.3 kg ha^{-1} yr^{-1}. Annual N input in the soil via leaf litter was 95.4 kg ha^{-1} yr^{-1}. During the sampling period (1995–2003) annual retranslocation usually fluctuated in the range of 3–10%. Weather conditions influenced significantly the use of nitrogen including retranslocation and the amount of N incorporated in litter. In drought year (1999 and 2002) it was significantly higher (23% and 20% of the leaf N pool, respectively).

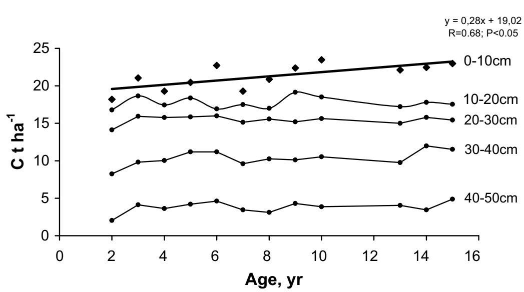

Fig. 4. The dynamics of soil carbon storage in different soil layers in grey alder stand.

The starting N pool of herbs in the 10-year-old stand was 6.2 kg ha^{-1}.

The total annual leaching of different forms of N was estimated at 14.9 kg ha^{-1} yr^{-1}. The main forms of leached N were nitrate (48.2%) and organic N (51.6%), the share of ammonium and nitrite N was negligible (0.1% of the total leached N flux for either). Maximum leaching occurred in autumn (September).

The overall average ± standard deviation flux of N_2O–N, calculated over all measuring times, was 0.14 ± 0.12 mg N_2O–N m^{-2} d^{-1}, varying from −0.01 to 0.60 mg N_2O–N m^{-2} d^{-1}. Significantly higher values were measured in July 2003 and in May 2005. The N_2–N flux for the whole study period was 20.2 ± 12.2 mg N_2–N m^{-2} d^{-1} and it varied from 10.8 to 1950 mg N_2–N m^{-2} d^{-1} for different replicates (Fig. 5). Approximation of these figures for the whole study area and for the whole year yields 0.50 ± 0.45 and 73.8 ± 44.5 kg N ha^{-1} yr^{-1} for the annual flux of N_2O–N and N_2–N, respectively. The average N_2:N_2O ratio was 171, which varied from 47 in July 2003 to 261 in December 2006.

The deposition flux was 6.4 kg ha^{-1} yr^{-1} as estimated at 35 km from the experimental area (Mander et al., 1997). In the present study it was assumed that deposition in the study area was as large as in the above study.

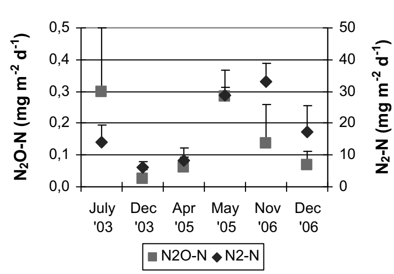

Fig. 5. Average and standard deviation values for nitrous oxide and dinitrogen fluxes from the study sites in 2003, 2005 and 2006.

Symbiotic nitrogen fixation calculated by balancing the fluxes of the N budget was 151.5 kg ha^{-1} yr^{-1}, which covered a significant proportion (74%) of the annual N demand of the plants (Table 2). Symbiotic fixation per 1 kg of nodule mass was 0.97 kg N yr^{-1}. The fluxes for the 5-year-old stand were estimated in earlier studies (Uri et al., 2003a, 2004).

4. Discussion

4.1. Nitrogen demand and storages

The lower annual nitrogen demand of the stand in the 10-year-old stand compared with the younger 5-year-old stand was caused mainly by the decrease in understorey biomass. Owing to the more closed and shading tree canopy, the N demand of the understorey was more than twice lower. During the period from 5 to 10 years of age the N demand of the trees increased 1.5 times; the increase in the N demand of the trees during 5 years is related to increased production of woody biomass, while the N demand of the foliage remained quite stable. Foliage mass stabilized in the 7-year-old stand (Uri et al., 2009) and a substantial proportion of nitrogen (70% of the above-ground N demand of the trees) accumulated in the leaves at both 5 and 10 years of age. The N demand was higher in the stand at age 5 years, which is in accordance with the results for riparian buffer grey alder stands (Mander et al., 2008). As the studied grey alder stand had not yet reached maximum productivity at the age of 10 years, CAP was still increasing and started to decrease probably at the age of 16–17 years (Uri et al., 2009) after which annual N use must have decreased as well. According to other reports, a maximum of CAP for grey alder stands occurs at the age of 5–15 years (Rytter, 1989, 1996; Johansson, 1999). As total N accumulation in the above-ground woody biomass of the 10-year-old stand amounted to 197 kg ha^{-1}, in the case of conventional harvesting (leafless above-ground part) N removal from the site would be modest in comparison with annual N_2 fixation or the soil N pools.

Data about below-ground biomass and nutrient content bound in the below-ground biomass of alders are scarce (Rytter, 1989; Bormann and Gordon, 1984); however relevant data about the fine root production of grey alders are practically lacking despite the evident importance of this flux in N or C budgeting. The total below-ground biomass of the coarse fractions and the below-ground part of woody biomass developed proportionately: when in the 5-year-old stand the course root fraction accounted for 19.1% of total woody biomass, then in the 10-year-old stand this proportion was similar, 18.8%. According to Lõhmus et al. (1996) the corresponding proportion was 19.8% in a 14-year-old riparian grey alder stand and 16.9% in a 40-year-old stand.

The grey alder stand invested a relatively small amount of N for developing the fine root system: in the 5-year-old stand the biomass of the fine roots was 550 ± 105 kg ha^{-1} and the biomass of the nodules 169 ± 76 kg ha^{-1} (Uri et al., 2002), while in the 10-year-old stand the respective values were 870 ± 140 and 156 ± 60 kg ha^{-1} (Uri et al., 2009). The biomass and the vertical distribution of the nodules remained unchanged during the 5 years of development.

Owing to intensive differentiation and self-thinning of the stand between the ages 5 and 10 years (12,660 trees per ha and 7400 trees per ha, respectively), the biomass of the fine roots per tree increased 2.7 times and the nodules per tree increased 1.6 times. Considering the stable biomass of the nodules at stand ages 5 and 10 years, it can be concluded that grey alder stand on former farmland has already formed an optimal biomass of the nodules by the age of 5 years to ensure sufficient symbiotic N_2 fixation. Owing to a fertile soil (*Eutric Podzoluvisol*), a significant share of the annual N demand both in the 5-year-old (Uri et al., 2003a) and in the 10-year-old stand was covered by NNM and, most probably, there was no need to increase the biomass of the nodules any more.

Regarding fine roots, we did not find any earlier literature data about the annual fine root production of grey alder. The fine root production in the studied grey alder plantation was low; in certain conditions the proportion of below-ground production may attain 75% of total annual production (Jackson et al., 1997). Developing young grey alder ecosystems apply both extensive and intensive fine root strategies to improve mineral nutrition (Lõhmus et al., 2006b). Trees using an extensive strategy increase the mass, surface area and length of the fine roots, which leads to a simultaneous increase in the rhizosphere. When an intensive strategy is preferred, trees increase or maintain the efficiency of the fine roots and rhizosphere processes throughout the morphological adaptations of the fine roots (Leuchner et al., 2004), and/or the activity of root-associated microorganisms for plant mineral nutrition could be increased or maintained (Lõhmus et al., 2006a,b). In the studied stand the difference between the soil–root interface and bulk soil microbial activity and diversity was markedly higher than in grey alder stands growing on forest land (Lõhmus et al., 2006a). A possible explanation for this is that more assimilates are located below ground to support rhizosphere processes for effective nutrition. In present stand also specific root area (SRA; m^2 kg^{-1}) was significantly higher (Lõhmus et al., 2006b) than in natural alder stands, and it showed positive correlation with the activity of microbial communities. Hence both the low fine root biomass and turnover rate indicate the significantly greater role of the intensive fine root strategy in the studied grey alder stand.

4.2. Soil

The initial (1995) N pool in the upper 20 cm layer (2.70 t ha^{-1}) fits the range of the N pool in boreal forest ecosystems, being, as a rule, 1–8 t ha^{-1} (Gundersen, 1995). The total nitrogen pool in Estonian agricultural soils ranges between 3 and 9 t ha^{-1} (Kask, 1975). In the studied stand N content in the upper 0–10 cm soil layer increased during 14 years after establishment on an average 26.4 kg N ha^{-1} yr^{-1}. In comparison with a riparian grey alder stand where annual N accumulation in the soil was 98.3 kg N ha^{-1} yr^{-1} (Mander et al., 2008), this value is 3.5 times lower, probably partly due to the absence of the slope effect (input from the upslope area). However, according to Myrold and Huss-Danell (2003), net annual N accumulation in grey alder plots in a degraded soil at high latitudes was 0.3 and 9.4 kg N ha^{-1} yr^{-1}, i.e. 3–9 times lower than in our stand. According to Binkley (2005), in red alder-Douglas fir stands the value of N accretion varied from 25 to 78 kg N ha^{-1} yr^{-1} and according to DeBell and Radwan (1979) it was 80 kg N ha^{-1} yr^{-1} in a pure red alder stand. Hence the impact of site environmental factors, as well as stand density and age on N accumulation in the soil is crucial.

The significant increase in soil C content indicated essential C sequestration under the studied grey alder stand (Fig. 4). Increasing of soil C content in short-rotation forests or in forests with diminished rotation length has also been reported in other studies (Liski et al., 2001). Another important aspect which enhances the prospects of alder forests for short-rotation energy crops is their high capacity for adaptation in the conditions of elevated atmospheric CO_2. In most forest ecosystems, soil fertility limits C sequestration in a CO_2-enriched atmosphere (Oren et al., 2001; Heath et al., 2005). Several studies on *A. glutinosa* show, however, that elevated atmospheric CO_2 increased C assimilation activity (Vogel and Curtis, 1995) and enhanced significantly the growth of alders (Vogel et al., 1997; Bucher et al., 1998; Temperton et al., 2003). It has been shown that elevated atmospheric N deposition makes a minor contribution to C sequestration in temperate forests (Nadelhoffer et al., 1999), however, in our plantation the deposition input covered only 3.9% of the plant's demand.

The soil acidifying effect of the alders was highly evident. During the 14-year period soil acidity increased 1.3 units in the upper 0–10 cm topsoil layer. Addition of fast decomposable litter-N into the soil increases the intensity of nitrification, which is a strong acidifying process. The pH decreased both due to symbiotic nitrogen fixation and high nitrification rate (100%). Soil acidification was also revealed in the deeper soil layer (40–50 cm) (Fig. 3) where soil pH decreased up to 1.0 unit ($R = 0.91$; $P < 0.05$). The decrease in pH was intensive during the first 7 years, and after canopy closure the acidifying effect declined. According to earlier studies on black alder stands growing on exhausted mining areas, soil pH decreases 1–2 units during the first 25 years of stand development and the acidifying effect decreases with increasing stand age, being the highest in the first year after planting when the pH of the rhizosphere is 1.3–1.5 units lower than that of non-forested area (Lõhmus et al., 2006a). In the red alder stand nitrification is a considerable source of acidity (Van Miegroet and Cole, 1985). In the case of *A. rubra* a strong negative effect of soil pH was observed during a 50-year rotation period (Cole et al., 1991); in this case the second forest generation of alders at same site may be less productive. These results confirm the soil acidifying effect of alders. Hence site characteristics and previous land use may strongly affect the soil acidification process. The effect of annual meteorological conditions was clearly revealed for soil pH (Fig. 3). In the exceedingly drought years (1999 and 2002) soil pH increased. This can be explained by a decrease in NNM and net nitrification due to soil water deficiency. Another reason may be diminished N_2 fixation and limitation of available assimilates as both above-ground production and leaf biomass decreased in the drought years.

To mitigate acidification of soils, an optimal scheme of rotating alders with other fast growing but non-leguminous and/or non-actinorhizal trees should be worked out. Also, liming could produce a positive effect (Gundersen et al., 2006) and, finally, some ecotechnological measures as establishment of constructed wetlands downhill of alder plantations to mitigate off-site movement of nitrates can solve the problem in some cases (Kuusemets and Mander, 1999).

4.3. Nitrogen fluxes

Annual NNM in the studied stand in the upper 0-20 cm layer accounted for 60.4% of the annual demand of the vegetation (alders and herbs) in the 10th year after planting. The flux of annual NNM can be considered relatively high, as for deciduous stands this parameter usually ranges between 50–150 kg ha^{-1} (Aber et al., 1989). Usually, the NNM flux is high in grey alder stands because leaf litter is easily degradable, N content is high in decomposing leaves, varying between 20 and 40 g kg^{-1} (Rytter, 1990; Saarsalmi, 1995; Uri et al., 2003b), and the C:N ratio is favourable. The possible impact of the previous use of land as agricultural land on the intensity of nitrogen transformation processes in the soil cannot be excluded (Uri et al., 2008). At the same time, the annual NNM flux in the grey alder stand was stable during stand development (from age 5 to age 10 years): in the 0–20 cm soil layer formed 141 kg ha^{-1} yr^{-1} in the 5-year-old stand and 124 kg^{-1} ha^{-1} in the 10-year-old stand, which is consistent with the decreased annual demand of the forest ecosystem.

Nutrient retranslocation from senescent leaves is an essential adaptation of trees for efficient nutrient use. As resorption efficiency increased in the drought years (1999 and 2002), the increased resorption of N from senescing leaves is one mechanism by means of which alders increase their NUE in response to unfavourable conditions. When the drought years were excluded, average resorption efficiency was 3-11%, which is accordance with the values estimated for natural grey alder stands (8–14%) (Mander et al., 1997). For *A. glutinosa*, average decrease in leaf nitrogen concentration before autumn was 16% (Dawson and Funk, 1981).

Litter N input into the soil was mainly affected by foliage mass, which stabilized at 3 t in the 7-year-old stand. The annual litter N flux decreased in the drought years due to decreased leaf production (Fig. 1). Because the amount of nitrogen introduced annually in to the soil by leaf litter can vary significantly depending on growth conditions, stand age, etc., the results presented in the literature differ a great deal and vary from 12 to 300 kg ha^{-1} yr^{-1} (Tarrant and Trappe, 1971; Binkley, 1981; Rytter, 1989; Turner et al., 1976).

Maximum N leaching occurred in autumn, in September. Leaching was most probably promoted by intensive decomposition of leaf and herb litter, which induced N release. Decomposition was promoted in a warm and rainy autumn. At the same time, nutrient uptake by the plants (alders + herbs) ceased at the end of the vegetation period. Estimated leaching (14.9 kg ha^{-1} yr^{-1}) formed quite a modest flux in the total N budget. According to literature data, nitrogen can leach from natural red alder-conifer mixed stand in the amount of 5-50 kg ha^{-1} yr^{-1} (Binkley et al., 1992) and essential nitrate leaching may occur after harvesting of mature alder stand (Van Miegroet et al., 1992). Nitrogen leaching of 9–13 kg ha^{-1} yr^{-1} was observed in riparian grey alder stands functioning as buffer zones (Mander et al., 1997). Taking account of the amount of accumulated N in the deeper soil layer (215 kg ha^{-1}) during the observation period (14 years), it can be supposed that actual leaching from the ecosystem is smaller. The N leached to the deeper soil layers will most probably be immobilized there, however, denitrification loss from the deeper soil layers cannot be excluded (Persson and Wirén, 1995).

The values of the N_2O flux were comparable to those reported in similar studies from the riparian grey alder stands, varying from 0.2 to 0.7 kg N_2O–N ha^{-1} yr^{-1} (Teiter and Mander, 2005; Mander et al., 2008). A decrease in nitrous oxide emission as well as an increase in the dinitrogen flux during the succession of alder stands, reported for riparian grey alder stands (Mander et al., 2008), is most probably a typical temporal pattern of gaseous N fluxes until grey alder stand reaches maximal possible age (40–50 years). However, approximation of gaseous nitrogen emission for the whole year based on four measurements is questionable since there is a seasonal trend in both N_2O and N_2 fluxes (see Maljanen et al., 2010a,b). On the other hand variability of N_2O fluxes from the agricultural soils can be significantly higher than observed in our study. It can vary from 0.01 kg N_2O–N ha^{-1} yr^{-1} on arable automorphic soils up to 34 and 64 kg N_2O–N ha^{-1} yr^{-1} on bare peat (Maljanen et al., 2004) and ploughed peatland in thawing-freezing regime (Priemé and Christensen, 2001), respectively.

Since alders fix N_2, a large part of the annual N demand may be covered from atmospheric nitrogen; literature data about atmospheric N fixation of alders vary in a broad range (Binkley, 1981). Nitrogen fixing capacity may depend on many factors such as differences between alder species, biomass of nodules (Binkley, 1981; Rytter, 1989), soil properties (Johnsrud, 1978), stand densities (Bormann and Gordon, 1984), and stand age (Lõhmus et al., 2002). In a 30-year-old grey alder stand it can be as high as 43 kg N ha^{-1} yr^{-1} (Johnsrud, 1978). In a young, 4-year-old, *A. rubra* stand up to 70% of accumulated nitrogen can originate from symbiotic fixation (Tripp et al., 1979). A 14-year-old natural riparian grey alder stand can fix up to 185 kg N ha^{-1} yr^{-1} from the atmospehere and a 40-year-old heavily polluted mature riparian grey alder stand can fix 28 kg N ha^{-1} yr^{-1} (Lõhmus et al., 2002). For *Alnus nepalensis*, annual N fixation increased from the age of 5 years

($52\,kg\,ha^{-1}\,yr^{-1}$) peaking at the age of 15 years ($155\,kg\,ha^{-1}\,yr^{-1}$) and decreased with increasing plantation age (Sharma et al., 2002). Cote and Camire (1984) reported a maximum rate of N-fixation of $53\,kg\,ha^{-1}\,yr^{-1}$ in pure black alder stands. In the present study symbiotically fixed N ($151.5\,kg\,ha^{-1}\,yr^{-1}$) is average considering reported values. Yet it can be a maximum value for this stand owing to stabilization of leaf mass production and maximization of stand biomass productivity.

5. Conclusions

Land use change from abandoned agricultural land to grey alder stand is ecologically relevant. Several soil changes caused by the transition of the ecosystem from field to forest appeared to be fast. Owing to symbiotic dinitrogen fixation, afforestation of abandoned agricultural land by grey alder affects significantly N cycling and the soil N status. Annual symbiotic nitrogen fixation in a 10-year-old grey alder stand growing on abandoned agricultural land covered an essential part of the plants annual N demand. Despite the marked N input into the new forest ecosystem, possible environmental risks as leaching or N_2O emission were negligible. Gaseous N emission was considerable but nitrogen was emitted mainly in the form of N_2.

As there occurs appreciable carbon sequestration in the topsoil layer, grey alder stand on abandoned agricultural land acts as a C sink both for soil and tree biomass.

Soil acidification that was revealed during stand development is the only negative process but it can be easily mitigated by liming or by using silvicultural treatments, e.g. growing of next forest generations using non N_2-fixing species.

Grey alder is a potential resource of bioenergy and large scale establishment of alder stands on abandoned fields does not involve appreciable environmental risks.

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Long-term study of above- and below-ground biomass production in relation to nitrogen and carbon accumulation dynamics in a grey alder (*Alnus incana* (L.) Moench) plantation on former agricultural land

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Abstract

In the Northern and Baltic countries, grey alder is a prospective tree species for short-rotation forestry (SRF). Hence, knowledge about the functioning of such forest ecosystems is critical in order to manage them in a sustainable and environmentally sound way. The 17-year-long chronosequence study is conducted in a grey alder plantation growing on abandoned agricultural land. The results of above- and below-ground biomass and production of the 17-year-old stand are compared to the earlier published respective data from the same stand at the ages of 5 and 10 years.

The objectives of the current study were to assess 1) above-ground biomass (AGB) and production; 2) below-ground biomass: coarse root biomass (CRB), fine root biomass (FRB) and fine root production (FRP); 3) carbon (C) and nitrogen (N) accumulation dynamics in the Holvandi grey alder stand growing on former arable land. The main results of the 17-year-old stand were: AGB 120.8 t ha^{-1}; current annual increment (CAI) of the stem mass 5.7 t ha y^{-1}; calculated CRB 22.3 t ha^{-1}; FRB 81±10 g m^{-2}; nodule biomass (NB) 31±19 g m^{-2}; fine root necromass (FRN) 11±2 g m^{-2}; FRP 53 g DM m^{-2} y^{-1}; fine root turnover rate (FRT) 0.54 y and fine root longevity 1.9 y. FRB was strongly correlated with the stand basal area and stem mass. Fine root efficiency (FRE) was the highest at the age of 10 years; at the age of 17 years it had slightly reduced. Grey alder stand significantly increased N and C_{org} content in topsoil. The role of fine roots (FR) for the sequestration of C is quite modest compared to leaf litter C flux.

Keywords: grey alder, Alnus incana, fine roots, biomass production, nitrogen, carbon

Introduction

The EU 20-20-20 strategy (Directive 2009/28/EC) foresees an increase in the share of renewable energy to 20% by 2020. One possible means to reach the goal is to utilize woody biomass from short-rotation forestry (SRF) plantations more extensively. SRF is a silvicultural practice employing high-density plantations of fast-growing tree species on fertile land (Weih 2004). Woody biomass from SRF plantations may have great potential as a CO_2 neutral replacement for fossil fuels (Hall and House 1994; Tuskan and Walsh 2001).

Grey alder (*Alnus incana* (L.) Moench) is one of the most prospective fast-growing tree species in Scandinavia and the Baltic countries for SRF. Several studies demonstrate that grey alder is a suitable tree species for SRF in Estonia (Uri *et al*. 2002, 2003, 2009). This species is highly productive both on mineral and organic soils (Granhall and Verwjist 1994; Saarsalmi 1995; Rytter 1996; Telenius 1999). It is estimated that there are 385–472 million ha abandoned arable land suitable for SRF plantations in the world (Campbell *et al*. 2008). In Eastern Europe, the increase of such areas after the collapse of the USSR has been significant (Mander and Palang 1994; Astover *et al*. 2006; FAO 2008; Henebry 2009). Furthermore, grey alder as an actinorhizal N_2-fixing tree species can be used effectively for the biological fertilization of soil with N (Granhall 1994).

To understand the functioning of grey alder stands, it is crucial to study all forest ecosystem components, including the below-ground part of stands. Since the beginning of the current century, different aspects of the functioning of grey alder ecosystems have been studied in Estonia (Uri *et al*. 2002, 2003, 2009, 2011; Vares *et al*. 2003; Lõhmus *et al*. 2006; Aosaar and Uri 2008; Mander *et al*. 2008; Aosaar *et al*. 2011). Special attention should be paid to fine roots (d<2 mm) due to their importance in water and mineral nutrient uptake and the synthesis of certain growth hormones (Makita *et al*. 2011). Although the fine roots of forest trees make up less than 2% of tree biomass (Brunner and Godbold 2007), they may account for up to 75% of the annual net primary production (NPP) in mature forests (Helmisaari *et al*. 2002; Gill and Jackson 2000; Vogt *et al*. 1996). Thus, fine roots contribute significantly to the functioning of forest ecosystems and the below-ground accumulation of C. More adequate data on below-ground biomass and fine root turnover of different tree species are important in order to estimate soil carbon storage and fluxes, to specify the role of fine roots in the carbon cycle of forests (Gill and Jackson 2000) and to prepare carbon budget models.

The variability of below-ground biomass estimates is higher than that of above-ground biomass estimates due to the methodological difficulties related to studying root system components (Akkermans and van Dijk 1976; Sharma and Ambasht 1986; Rytter 1989; Tateno *et al*. 2004; Hendricks *et al*. 2006; Coleman 2007; Helmisaari *et al*. 2007; Sakai *et al*. 2007). Thus, variation in root productivity data among different stands could either reflect methodological differences or real differences in productivity (Hertel and Leuschner 2002; Finer *et al.* 2011a). The most common approaches to determining the FRB and FRP of fine roots in the field have been the sequential coring method (Vogt and Persson 1991; Ahlström *et al*. 1988; Helmisaari *et al*. 2002), the in-growth core method (Persson 1983; Makkonen and Helmisaari 1999) and the minirhizothron method (Majdi and Nylund 1996; King *et al*. 2002). In recent years the new prospective root mesh method (Hirano *et al*. 2009; Lukac and Godbold 2010) has been introduced.

Species of actinorhizal *Alnus* that fix atmospheric nitrogen (N_2) through the metabolic activity of the filamentous bacterial symbiont *Frankia* play an important role in the nitrogen cycle of temperate forest ecosystems

(Tjepkema *et al*. 1986; Baker and Schwintzer 1990; Huss-Danell 1997; Dawson 2008). Measuring nodule biomass is essential for estimating the amount of N_2-fixation (Tobita *et al*. 2010).

New knowledge of FRB and NB dynamics and FRP and FRE is needed for the better understanding of a highly productive alder forest ecosystem development and functioning. So far only a few scientific studies have been published reporting the fine root data of grey alder (Rytter 1989; Elowson and Rytter 1993; Uri *et al*. 2002, 2009). The current study presents the results of FRB, NB, FRP and FRE dynamics throughout the development of the grey alder stand (age 5 to 17 years).

The chronosequence approach is commonly used to study and model stand development dynamics. However, the variability of abiotic and biotic factors (soil properties; water regime; stand density; stand management; etc.) in the chronosequence of study sites cannot be avoided completely. Hence, the apparent advantage of the current paper is that the 17-year period of fine root and nodule growth dynamics along with thorough background data about soil properties and stand characteristics is presented as a continuous time series. Furthermore, the new knowledge presented is a prerequisite for compiling carbon accumulation and nutrient budgets in similar stands.

The hypotheses of the study were: (1) grey alder is a highly productive species suitable for SRF; (2) FR play an important role in C and N budgets; (3) there is a strong relationship between the above- and below-ground parts of the stand.

In order to verify the hypothesis, the objectives of the study were (1) to estimate the AGB production capability of grey alder; (2) to estimate the dynamics of the grey alder CRB, FRB, NB and FRP in a short-rotation plantation growing on former arable land; (3) to estimate the role of tree roots in the N and C sequestration in soil; (4) to study the relations between the above- and below-ground parts of the trees in the stand at different ages.

2. Material and methods

2.1 Study area and stand characteristics

The research area is located in the South-Eastern part of Estonia (58°3′ N; 27°12′ E). According to data from the meteorological station (Võru) closest to the experimental area, the mean annual temperature is 6 °C, the mean precipitation is 653 mm and the mean length of the vegetation period is 191 days. The plantation was established on abandoned agricultural land in spring 1995. The area of the stand is 0.1 ha. The soil is classified as *Eutric Podzoluvisol* (according to the FAO classification) (Table 1). One-year-old transplants of natural origin were used for planting. The survival and growth of the planting stock of different origins has been described previously (Uri *et al*. 2002; 2003). Before the establishment of the plantation, the area had been out of use for 2 years. No soil preparation, weed control, fertilization or other treatment was performed before or after planting. The initial density was 15,750 trees per hectare.

The data of above- and below-ground (Table 2 and 3) characteristics of the stand at the age of 5 and 10 years has been published earlier (Uri *et al*. 2009); the respective data of the 17-year-old stand is original.

Table 1. Soil characteristics of the studied stand in the upper 10 cm soil layer. Presented: the average significant differences (indicated by different letters) according to the Tukey HSD test (P<0.05)

Age, y	N, %	C, %	Texture	pH_{KCl}	Organic matter, %
5	0.108^{a}	1.59^{a}	loamy sand	5.37^{a}	2.74^{a}
10	0.136^{b}	1.80^{b}	loamy sand	5.07^{b}	3.10^{b}
17	0.134^{b}	1.86^{b}	loamy sand	4.77^{c}	3.23^{b}

2.2 Estimating above-ground biomass and production

All the stand characteristics and AGB were always determined at the end of August, when the dimensions of the trees and the biomass had reached their annual maximum (Table 2). All the presented values reporting mass units throughout the article are given in dry mass (DM).

The AGB of the stand was estimated by using dimension analyses (Bormann and Gordon 1984) and has been described in detail in earlier studies (Uri *et al*. 2002, 2009). The stem breast height diameter ($D_{1.3}$) was measured in case of all trees. The trees were divided into five classes on the basis of $D_{1.3}$, and a model tree was selected randomly from each class. A total of seven model trees were felled in order to determine the above-ground biomass of the stand – one tree from each diameter class and one additional model tree from two diameter classes which presented a larger number of trees growing in the stand. The model trees were divided into sections and in every section, the mass and share of stemwood, stembark, branches and leaves was found.

To avoid the edge effect, model trees were selected from the middle of the study area.

The annual production of the stemwood, bark and branches was calculated as difference between the masses of the current and the previous year (Uri *et al*. 2002, 2009).

2.3 Estimating coarse root biomass and production

The coarse root biomass (CRB) (d>2mm) of grey alder trees is calculated on the basis of earlier studies by Lõhmus *et al*. (1996) and Uri *et al*. (2009), in which the CRB of a grey alder stand at the ages of 5, 10 and 40 years was estimated by excavating the root systems of model trees. In the studies referred to above, the share of coarse roots of the above-ground leafless biomass was found to be approximately 19%. Based on earlier results, it is assumed here that AGB and CRB develop proportionally. Hence, CRB and the share of CRB production in the current year of total CRB were calculated as follows (1 and 2, respectively):

$$CRB\ (t\ ha^{-1}) = (AGB_{leafless}) * 0.19; \qquad (1)$$

$$CRB_{prod}\ (\%) = AGB_{prod} / AGB. \qquad (2)$$

2.4 Estimating the biomass and production of fine roots and nodules

2.4.1 Soil core method

In this paper, only the FRB and FRP of trees are estimated; the respective values of understory vegetation are not included in study. In this study, fine roots are defined as roots with a diameter of <2 mm.

The soil coring method (Vogt and Persson 1991) was used to estimate the biomass and necromass of fine roots and nodules of grey alder. The coring was always carried out in October. The number of samples: 20 in 1998 (stand age 5 years), 25 in 2003 (10) and 20 in 2010 (17). The results of the years 1998 and 2003 are presented in Uri *et al*. 2002 and 2009, respectively.

Soil cores were taken randomly from the whole area of the plantation with a cylindrical soil auger (diameter of the cutting edge 48 mm). Soil cores were divided into four equal 10 cm layers to a depth of 40 cm, placed in polyethylene bags and kept frozen until further processing. Alder roots and nodules were washed out of the soil cores during one week after sampling. Further, the fractions of living and dead fine roots and nodules were separated under a binocular microscope and cleaned from soil particles. The samples were dried at the temperature of up to 70 °C and weighed with the accuracy of 0.001 g. Soil core data was used to calculate the biomass of fine roots and nodules per hectare, summing up the average values for successive soil layers from the soil cores. The share of fine roots and nodules of the root systems was calculated.

2.4.2 In-growth cores

Altogether 150 in-growth cores (d=40 mm, mesh size 6 mm) were inserted into the soil to estimate fine root growth dynamics and FRP. The cores were inserted in five random transect groups all over the stand, into the topsoil to a depth of 30 cm in October 1999 (stand age 6 years). The meshes were filled with sieved root-free soil according to the genetic horizons of the soil. A total of 105 in-growth cores were extracted during 2000–2003: 7 samplings and 15 meshes per sampling. Samplings were carried out in November 2000; June, August 2001; June, August, November 2002; and June 2003. In November 2001, sampling was skipped due to the fact that the soil was frozen. All the subsamples obtained were transported to the laboratory and stored frozen (-18 °C) until processing. In the laboratory, soil cores were divided into depth layers of 0–10, 10–20 and 20–30 cm. Roots and nodules were carefully washed out of the soil. The fractions of fine roots and nodules were separated and cleaned from soil particles under a binocular microscope. Dead roots and nodules were separated as well. The samples were dried at a temperature of up to 70 ^{o}C and weighed with the accuracy of 0.001g.

Total FRP was calculated on the basis of in-growth core data and by balancing the biomass compartments of living and dead roots according to the decision matrix of Fairley and Alexander (1985). The FRP was calculated on the basis of FRB data from June 2002–June 2003. It included four samplings: June, August and November 2002 and June 2003. Root turnover rate (y^{-1}) was calculated from in-growth cores as annual root production (g m^{-2} y^{-1}) divided by the mean FRB (g m^{-2}). To avoid large fluctuations during the vegetation period, mean FRB was used to calculate the fine root turnover rate (Ostonen *et al*. 2005).

The FRP values for the 5- and 17-year-old stand were calculated using the same fine root turnover rate (FRT) (0.54 y) as was used in case of the 9-year-old stand. As the estimation of FRB and FRP is very labor-intensive, it was assumed that FRT is a stable and stand-specific parameter. The assumption is based on Finer *et al*. (2011a), who state that the variation of the FRT of trees can be explained neither with environmental nor with stand-related factors and that the FRT is species-specific.

Fine root efficiency (FRE) (t t^{-1} y^{-1}) was calculated by dividing the CAI with the FRB.

2.5 C and N storages

The N and C pools in the below-ground biomass of the stand were calculated by multiplying the biomass of root fractions with the respective N or C concentrations in the fractions. The weighted average was used in order to calculate average N and C concentrations in CRB; the fraction percentage was multiplied by the respective concentration. The ash content, which was <10% in all cases, was determined to check the possible soil contamination of roots.

N and C storage in soil was calculated on the basis of soil bulk density and the mean concentration of N or C in soil. Soil bulk density was determined in 2002 from 10 soil pits reaching to a depth of 50 cm. The density samples were taken with a stainless steel cylinder (d=40mm; volume 50.24 cm^3) from different soil layers (0–10 cm; 10–20 cm; etc.), three samples from each layer. After drying at the temperature of 105 ^oC, soil samples were weighed.

Soil N and C concentrations were studied annually in October 1995–2010 (stand age 2–17-years) when plant growth had ceased. Samples from soil layers were taken in ten random points at the depths 0–10; 10–20; 20–30; 30–40 and 40–50 cm and three composite samples were formed from each depth layer.

C and N input into soil via leaf and fine root litter was included in the study.

The N and C input flux into soil was calculated on the basis of foliage biomass and NC concentrations of collected leaf litter from an earlier study period (10-year-old stand). The litter was collected twice a month from 10 litter traps with the area of 0.25 m^2 each located randomly all over the plantation.

Root litter was considered as the dead fine root mass estimated in case of in-growth cores.

2.6 Chemical analyses

Nitrogen (N) and carbon (C) were determined from root and nodule samples. Tecator ASN 3313 was employed to test total N (Kjeldahl) in soil samples. Plant samples were analysed for total N by the Kjeldahl method using a Kjeltec Auto 1030 analyser. The dry combustion method was used with a varioMAX CNS elemental analyzer (ELEMENTAR, Germany) to test the C content in oven-dried plant material samples. Soil pH in 1M KCl suspensions was measured with the ratio of 10 g : 25 ml. Total C content in soil was determined by the dry combustion method using a varioMAX CNS elemental analyzer (ELEMENTAR, Germany). The analyses were carried out at the Biochemistry Laboratory of the Estonian University of Life Sciences.

On the basis of average concentrations, the total N and C accumulation in fine root and nodule biomass and the C and N input via leaves and fine roots into the soil were calculated.

2.7 Statistical methods

The normality of the variables was checked with Lilliefors and Shapiro-Wilk tests. The data of model trees were analysed by means of regression analysis. So as to find allometric relationships (1), $D_{1.3}$ served as the independent variable in all cases. The statistical significance of differences in biomass on different years between respective layers was checked with the t-test (Two-Sample Assuming Unequal Variances). There was no autocorrelation of the FRB data (d=2.2), which was checked with the Durbin-Watson test. The software STATISTICA 7.1 was used and the significance level $\alpha = 0.05$ was accepted in all cases.

3. Results

3.1 Above-ground biomass and production

The increase of AGB has been vigorous, exceeding 100 t DM ha^{-1} in the 17-year-old stand. The CAI of the 16-year-old stand was 14.2 t DM ha^{-1}, which is an impressive value, considering the conditions in Estonia. However, in the next growing season, it underwent a drastic decline (Table 2). The average mass of a single stem in the 16- and 17-year-old stand was 18.6 and 20.7 kg DM, respectively. The leaf mass as well as the leaf area index stabilized after the 5-year growth of the stand. The leaf mass has been fluctuating around 3 t DM ha^{-1} ever since (Table 2).

Table 2. Grey alder stand characteristics and above-ground biomass data: leaf area index (LAI); mean annual increment (MAI); current annual increment (CAI)

Stand characteristics

Age, y	Mean height, H, m	Mean $D_{1.3}$, cm	Basal area, m^2 ha^{-1}	Density, trees ha^{-1}	LAI, m^2 m^{-2}
5	4.6	2.6	7.4	12,700	2.2
10	9.5	5.7	20.7	7,400	4.0
16	13.9	8.7	35.2	5,360	4.2
17	14.3	9.3	37.6	5,100	3.8

Above-ground biomass

Age, y	Stem, t ha^{-1}	Leaves, t ha^{-1}	Branches t ha^{-1}	Total, t ha^{-1}	MAI, t ha^{-1}y^{-1}	CAI, t ha^{-1}y^{-1}
5	8.1	2.0	2.2	12.3	1.6	3.3
10	41.0	3.0	5.4	49.4	4.1	6.4
16	99.7	3.2	13.9	116.8	6.2	14.2
17	105.4	3.3	12.1	120.8	6.2	5.7

3.2 Coarse root biomass and production

The largest share of CRB formed from stump and the fraction d>10mm, being 9 t ha^{-1} and 7.8 t ha^{-1}, respectively (Table 3). To estimate the N and C accumulation in below-ground biomass, N and C concentration values from the 10-year-old stand were used (Table 3). The calculated CRB for the 16- and 17-year-old stand exceeded 20 t ha^{-1} (Table 4). The calculated coarse root productions values were 3.2 t ha^{-1} and 0.7 t ha^{-1} for the 16- and 17-year-old stand, respectively (Table 4).

Table 3. Coarse root biomass and N and C concentrations (mean ± standard error) in the 17-year-old Holvandi grey alder stand

Fraction	Share of coarse root biomass, %	Coarse roots biomass, t ha^{-1}	N, %*	C, %
Stump	40.4	9.0	0.4±0.3	51.46±0.13
Coarse roots d>10 mm	35.1	7.8	7.9±0.7	49.89±0.03
Coarse roots 5<d≤10 mm	10.7	2.4	9.1±0.5	49.73±0.04
Coarse roots 2<d≤5 mm	13.8	3.1	10.0±0.2	49.73±0.03
Total	100	22.3		

* data from Uri *et al*. 2011

3.3 Fine root standing biomass and necromass on the basis of soil cores

The total standing FRB in the 17-year-old grey alder stand was estimated to be 81±102 g m^{-2}. It has increased 32% compared to the 5-year-old stand. Compared to the 10-year-old stand, FRB was virtually the same (Table 4); the slight decrease in FRB was statistically insignificant (t-test; P=0.14). The difference between FRB in the 5- and 10-year-old stand in the upper 0–10 cm soil layer was statistically significant (P<0.05).

Table 4. Fine root and nodule biomass and necromass (mean ± standard error) dynamics in grey alder stand growing on abandoned agricultural land

Stand age, y	Coarse root biomass, t ha^{-1}	Coarse root production, % of biomass* / t ha^{-1}*	Fine root biomass, g m^{-2}	Fine root necromass, g m^{-2}	Nodule biomass, g m^{-2}	Nodule necromass, g m^{-2}
5	2.0	37.9 / 0.76	55±11	-	17±8	-
10	8.7	16.4 / 1.43	87±14	19±4	16±6	2±1
17	22.3*	3.3 / 0.33	81±10	11±2	31±19	1±1

* - Calculated

FRB in deeper soil layers has not changed significantly throughout the studied years (Figure 1). The principal share of FRB was always located in the upper 0–10 cm soil layer, remaining in the range of 47%–57% of the total fine root biomass. FRB in the upper 20 cm soil layer has increased gradually from 74% to 84% of total FRB with the increase in stand age.

The necromass of fine roots in the 10- and 17-year-old stand has remained quite stable, fluctuating between 10–20 g m^{-2} (Table 4). However, the relative share of necromass of FRB has decreased with increasing stand age, being 22% and 14% in 2003 and 2010, respectively.

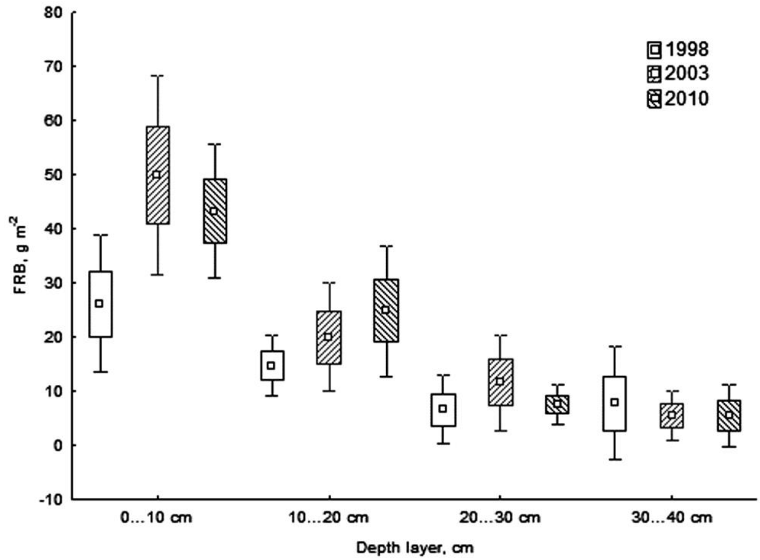

Figure 1. Vertical distribution of fine root biomass in grey alder stand in 1998, 2003 and 2010. The box indicates mean ± standard error; the whiskers indicate 95% confidence intervals

3.4 Fine root standing biomass in in-growth cores

FRB in in-growth cores was low during the first two growing seasons (the vegetation periods of 2000 and 2001) (Figure 2). After one growing season, in November 2000, the FRB was 15 g m^{-2} in 0–30 cm soil.

FRB was always highest in the upper 10 cm soil layer, forming 50% of the total biomass. The highest standing FRB for the 0–30 cm soil layer was 123 g m^{-2} in June 2002 (the third growing season after the installation of the cores). The mean biomass in meshes in the period June 2002–June 2003 was 98 g m^{-2}. The FRB value of June 2002 is not comparable to the autumn values due to the annual growth dynamics of fine roots (Figure 2). Since the in-growth core data reflected FRB data in soil layers with the depth of up to 30 cm, but the soil cores were up to 40 cm deep, we used the extrapolation of data. The share of standing biomass in soil cores in 2003 of the 30–40 cm soil layer was 7%. The respective values of standing biomass in June and November 2002 in in-growth cores would be 132 g m^{-2} and 66 g m^{-2}, respectively.

3.5 Net primary production of fine roots

FRP in the in-growth cores after the first growing year (October 1999–November 2000) was 15 g m^{-2} y^{-1}, being the most vigorous in the upper 10 cm soil layer (48% of the total). The calculation was made on the basis of the FRB in soil cores. Estimated FRP in the 9-year-old stand was 53 g m^{-2} y^{-1} and the calculated FRP values for the 5- and 17-year-old stand were 30 and 44 g m^{-2} y^{-1}, respectively.

In the 9-year-old stand, the turnover rate of fine roots was 0.54 y and longevity 1.9 y.

The FRP of very fine roots (d<1 mm) was 34 g m^{-2} y^{-1}; the turnover rate 0.50 y and the longevity 2.0 y in the 9-year-old stand.

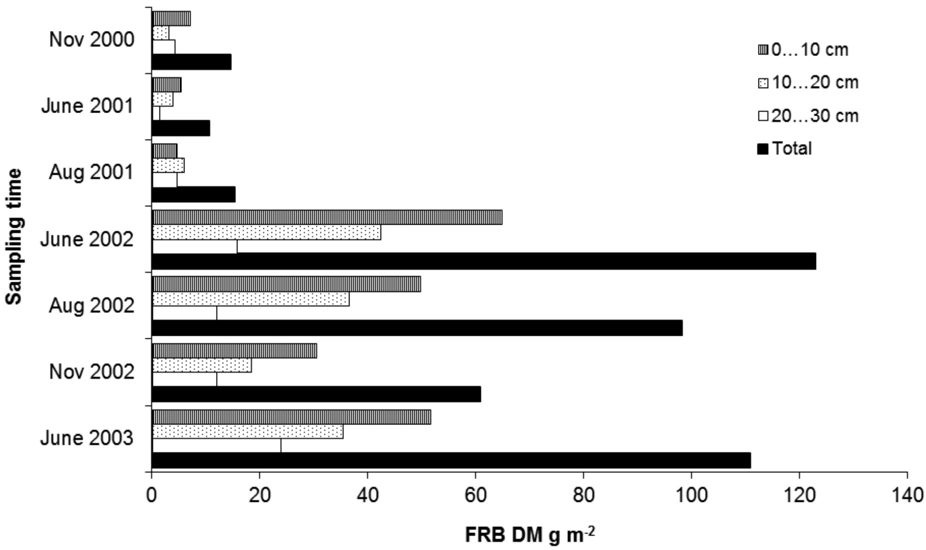

Figure 2. Fine root standing biomass dynamics in in-growth cores. Experiment installed in October 1999

3.6 Nodule biomass

The biomass of living nodules in the 17-year-old stand has doubled compared to respective values in the younger stand, reaching up to 31±19 g m^{-2} (Table 4). The biomass of nodules has accumulated in the upper 20 cm soil layer and half of it in the 10 cm topsoil. The depth distribution of the nodules has changed in the 17-year-old stand compared to earlier stages (Figure 3): in both the 5- and 10-year-old stand, approximately 80% of all nodules were located in the upper 10 cm soil layer. In the 17-year-old stand, the nodule depth distribution in the 0–10 and the 10–20 cm soil layer was equal. Almost no nodules have been found in deeper soil layers throughout the study period.

The average nodule biomass per tree increased with increasing stand age. In the 5-year-old stand, the average nodule biomass per tree was 13.4 g $tree^{-1}$; in the 10- and 17-year-old stand, 21.6 and 60.8 g $tree^{-1}$, respectively.

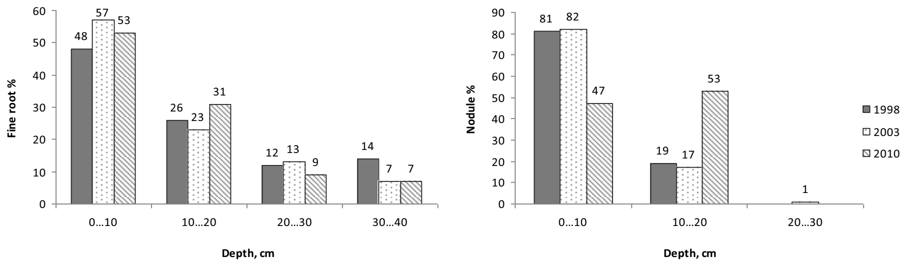

Figure 3. Dynamics of the relative vertical distribution of fine roots (d<2mm) and nodules in the 5-, 10- and 17-year-old grey alder stand on abandoned agricultural land. The data of the years 1998 and 2003 has been published earlier in Uri *et al*. (2009)

3.7 Relations between fine roots and above-ground stand characteristics

Significant correlation (R=0.78) between fine root standing biomass and the stand age as well as between FRB and stand basal area (R=0.77) were established (Figure 4). A very strong relationship (R=0.96) was found between stand age and average FRB per tree. As stand stem mass and stand basal area are strongly correlated characteristics, a similar correlation (R=0.78) exists between FRB and stand stem mass (Figure 5).

Fine root efficiency (FRE) was the highest at the stand age of 10 years (7.3 t t^{-1} y^{-1}). The respective values have been lower in the 5- and 17-year-old stand as well, being 5.9 and 7.0 t t^{-1} y^{-1}, respectively.

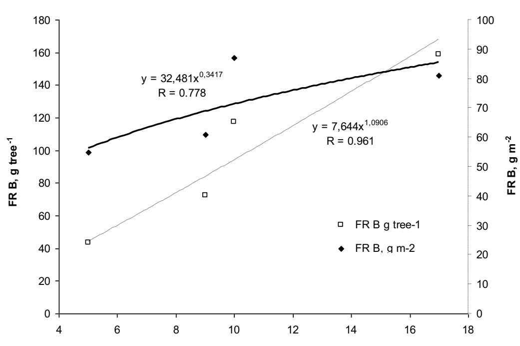

Figure 4. Relationship between the age and fine root biomass of the stand and average fine root biomass per tree in grey alder stand

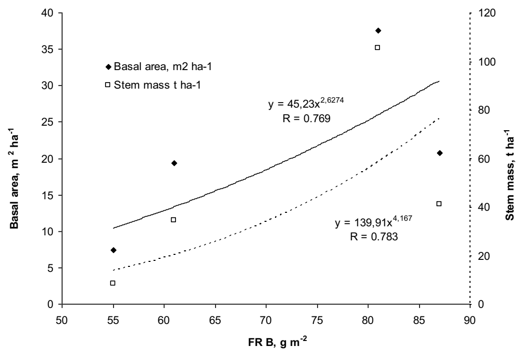

Figure 5. Relationships between the fine root biomass and basal area of grey alder stand; fine root biomass and stem mass

3.8 Carbon and nitrogen accumulation in the below-ground part of the stand

With the increasing age of stand, CRB has also increased (Table 4). Hence, the N and C storage in CRB increased during the stand development, reaching almost 70 kg ha^{-1} and 5 t ha^{-1} in the 17-year-old stand, respectively (Table 5).

The average nitrogen concentration of fine roots and nodules in the 17-year-old stand was 1.246±0.02% and 1.923±0.02%, respectively. The average C concentration in fine roots was 51.46±0.13%.

C accumulation in biomass peaked at the age of 10; the N and C accumulation in fine roots in the 17-year-old stand was also lower than the respective values in the 10-year-old stand (Table 5).

Table 5. Accumulation of nitrogen (N) and carbon (C) in coarse and fine root biomass and the annual production thereof in the upper layer of soil

Stand age, y	Accumulation in biomass kg ha^{-1}					Accumulation in annual production kg ha^{-1}				Storage in 0–10 cm soil layer t ha^{-1}	
	Fine roots		Nodules	Coarse roots		Fine roots		Coarse roots			
	N	C	N	N	C	N	C	N	C	N	C
5	6.9	282.6	3.3	13.6	988	3.7	154.1	5.2	374	1.38	20.5
10	10.8	447.0	3.1	59.4	4,299	6.7	277.5	9.7	705	1.74	23.5
17	10.1	416.2	5.9	68.9	11,000	5.5	226.1	2.3	165	1.72	24.3

Both N and C pools in soil have increased significantly during the development of the stand (Table 5). In the 17-year-old stand, the N and C flux via leaf litter was 112 kg ha^{-1} and 1,635 kg ha^{-1}, respectively. The respective numbers of fine roots are 2.6 kg ha^{-1} and 144 kg ha^{-1}.

Discussion

Above-ground part of the stand

The estimated AGB of the stand is very high for the conditions in Estonia as well as other Baltic and Scandinavian countries. Stem volume in the stand, calculated from the stemwood density of 396 kg m^3 (Aosaar *et al*. 2011), is 266 m^3 ha^{-1} in the 17-year-old grey alder stand. The result exceeds the highest values of the grey alder yield-tables in Aosaar *et al*. (2012), in which the highest stand volumes at the ages of 15 and 20 years are 170 m^3 ha^{-1} (Latvia) and 225 m^3 ha^{-1} (Latvia, Norway), respectively. Extremely high stem volume results of single stands are reported from Central Sweden, where the stem volumes of 15-year-old stands growing on fine sand were 390 m^3 ha^{-1} and 368 m^3 ha^{-1} (Johansson 2000), calculated from the stemwood density of 359 kg m^3 (Johansson 2005). These numbers reflect the high biomass production potential of the grey alder.

The CAI in the 16-year-old stand was also extremely high – 18.8 t ha^{-1} y^{-1} (stem mass 14.1 t ha^{-1} y^{-1}). The result is comparable to the production numbers reported by Tullus *et al*. (1998) – 12.1 t ha^{-1} y^{-1} (6-year-old stand) and Granhall and Verwijst (1994) – 17.0 t ha^{-1} y^{-1} (5-year-old stand).

However, in the Holvandi stand, CAI decreases drastically at the age of 17 years. As grey alder bioproduction is very sensitive to the water deficit in the vegetation period, drough conditions in summer 2010 may have had a considerable impact on the growth of the stand. Further, the onset of bulk maturity is expected to occur at the stand age of 15–20 years, as pointed out by many authors (Lõhmus *et al*. 1996; Rytter 1995; Rytter *et al*. 2000; Daugavietis *et al*. 2009; Uri *et al*. 2009) and it is in good accordance with several yield-tables reported in Aosaar *et al*. (2012), which leads to the decrease in CAI. Hence, the drastic decrease in CAI is probably caused by the concurrence of the inherent growth-reducing period and unfavorable weather conditions.

The question of initial stand density and stand density in mature age is of crucial importance in respect of SRF stands. In the Holvandi stand, the initial density was high (15,750 ha^{-1}), which is characteristic of natural grey alder stands. In case of a plantation, such initial density can be considered irrational due to the high costs related to the establishment of the plantation. In literature, there is almost no data about the thinning of grey alder stands. However, according to an experiment by Rytter (1995), thinning is not essential to achieve the higher bioproductivity of the alder stand, since an equal amount of obtainable biomass was produced both in thinned and unthinned stands. The density of the Holvandi stand at the age of 17 years was 5,100 ha^{-1}; neither thinnings nor other silvicultural treatments were implemented throughout the growth of the stand. However, the density of 5,100 ha^{-1} can be considered optimum since it is in good accordance with the stand density values of most productive yield-tables reported in Aosaar *et al*. (2012), in which, at the age of 15, density ranged from 2,700 ha^{-1} to 6,500 ha^{-1}. Hence, it may be assumed that similar stand volumes would have been produced in case of the lower initial density of the plantation.

Below-ground part of the stand

In the 5-year-old stand, FRB was 55±11 g m^{-2} (Uri *et al*. 2002) and FRB per tree was 43.3 g. Compared to the younger stand, FRB increased and remained stable in the 10- and 17-year-old stand. Although the FRB of stand stabilized, FRB per tree increased due to the natural self-thinning of the stand and following an increase in the dimensions of trees in order to meet their rising need for nutrients and water. However, the foliage mass stabilized after canopy closure in the level of 3–4 t ha^{-1} and the stem mass increment is gradually decreasing in older stands. Hence, the infinite enlargement of the fine root system is unnecessary for trees. However, on the basis of available data, it is impossible to predict the period of time needed for the stabilization of FRB per tree.

FRB in the grey alder plantation has remained at <1 t ha^{-1}. It seems to be an optimum FR supply for the grey alder stand growing on fertile soil, as there were no increases in the FRB value in the 17-year-old stand compared to the 10-year-old stand. The FRB value can be considered modest, as the mean FRB in boreal and temperate forests is 526±321 and 775±474 g m^{-2}, respectively (Finer *et al*. 2011b). According to Bloom *et al*. (1985), trees growing on poor sites should allocate a greater proportion of their resources into FRB than those growing on fertile sites. In a study by Kalliokoski *et al*. (2010), the FRB of *P. abies* and *P. sylvetris* increased with decreasing soil fertility, while the FRB of *B. pendula* remained the same. According to literature, nitrogen limitation in soil increased the FRB of different tree species (Finer *et al*. 2007; Helmisaari *et al*. 2007; Graefe *et al*. 2010). In the studied plantation, the N content in topsoil was high; the respective value has increased significantly in the 10- and 17-year-old stand, compared to the initial situation (Uri *et al*. 2011).

In November 2000, the FRB in in-growth cores was 0.15 t ha^{-1}, which can be also handled as FRP of the first growing year. In August 2001, the FRB in meshes was at the same level as it was in November 2000 (Figure 2). These values indicate very low FRP values during the first and second growing year. This is in good accordance with literature (Ostonen *et al*. 2005; Makkonen and Helmisaari 1999; Vogt *et al*. 1998), in which it is indicated that in absolute values, fine root biomass may still be lower during the second and third year in the in-growth cores. The FRB estimated from in-growth cores after the first or second year is significantly lower than the FRB in soil cores, i.e. the actual FRB in soil. FRB in in-growth cores fluctuates seasonally, reaching its peak in June and decreasing due to root mortality until the beginning of the next growing season (Figure 2).

Although the installing of in-growth meshes strongly modifies the disturbed environment of surrounding roots, it allows us to calculate FRP directly. Therefore, it is suitable for comparing FRP between sites or treatments (Messier and Puttonen 1993). Since the period of stabilization for in-growth cores is required (Ostonen *et al*. 2005) and roots are still expanding into the meshes in the third growing year (Makkonen and Helmisaari 1999), then the production, turnover rate and longevity of fine roots were calculated on the basis of samples taken in 2002 and 2003. FRP in our grey alder plantation was low (54 g m^{-2}), which may have been caused by the droughty summer (Nikolova *et al*. 2009). However, the proportion of below-ground production may attain 75% of total annual production (Jackson *et al*. 1997).

The longevity of fine roots in in-growth cores was calculated to be approximately two years and hence, FRN during the first two growing periods in cores was close to zero. The maximum FRB in in-growth cores was estimated in June 2002 (123 g m^{-2}); by November it had halved, so the mass of dead roots should have been relatively high. However, the mass of dead roots in in-growth cores in November 2002 was less than 1 kg ha^{-1}, i.e., the process of the decomposition of dead fine roots in the fertile sites of the grey alder plantation should be extremely rapid and nutrients and C captured in fine roots should reach the soil quickly.

The decomposition of organic matter, including fine roots, depends on environmental conditions and the nutrient composition of organic matter. The decreased C/N ratio stimulates the decomposition of organic matter (Vervaet *et al*. 2002; Scott and Binkley 1997). Due to the high content of N in fine roots (1.25 %) and the favorable C/N ratio, the decomposition of fine roots is rapid and the storage of dead fine roots in soil remains relatively low. Hence, the standing FRN in our study was always very low due to favorable decay conditions.

As grey alder is a N_2-fixing species, it is essential to estimate the biomass of nodules. The nodule biomass of *Alnus* species varies, depending on the tree size and stand density (Bormann and Gordon 1984), but also on the age of the stand (Sharma and Ambasht 1986; Son *et al*. 2007). Nodules can be several years old and grow to a large size (Akkermans and van Dijk 1976). Nodule biomass in the 5- and 10-year-old plantation was similar. However, both estimations are smaller than in the 4-year-old grey alder coppiced stand in Finland (25–29 g m^{-2}) (Saarsalmi *et al*. 1985). Bormann and Gordon (1984) found that the average mass of the nodules in a 5-year-old *Alnus rubra* stand was 15 g m^{-2}. In the 17-year-old stand, the NB value had doubled compared to the 10-year-old stand. However, the number of nodules was very low. NB in the 17-year-old stand was greatly affected by one single nodule (0.65 g) found in the 10–20 cm soil depth layer; only 2 nodules in total were found in the 10–20 cm soil layer. It differs from the younger stand (10 y), in which several nodules were found. With increasing stand age and bigger trees, the mean weight of nodules increases as the number of nodules decreases. This is in good accordance with Tobita *et al*. (2010), in which the size of nodules shifted from smaller to larger size classes with the increasing breast height diameter of trees. A very low number of nodules in deeper soil layers is reported in literature: In a study carried out in Estonia by Lõhmus *et al*. (1996), no nodules were found deeper than 10 cm; a similar tendency is described by Johnsrud (1978) in Norway; Elowson and Rytter (1993) reported the following nodule allocation – 98% were found in the upper 20 cm of the soil profile; according to Rytter (1989), more than 90% of the total mass of the nodules on intensively managed organic soil were contained in the upper 0–6 cm soil layer.

Furthermore, the increasing N content in soil increases nodule weight (Bond *et al*. 1954); the soil N content in the plantation has increased significantly over the years (Table 1). Hence, with increasing age and soil fertility, alders grow fewer nodules, which are larger, leading to greater variations in nodule biomass, as shown in Table 4.

Fine root efficiency (FRE) in the studied stand was the highest at the age of 9–10 years (in 2002–2003); at the age of 17 years, FRE had slightly decreased. The low FRB and FRP indicate the high activity of fine roots, which is described as intensive fine root strategy (Lõhmus *et al*. 2006; Ostonen *et al*. 2011). Trees using the extensive strategy increase the mass, surface area and length of fine roots. In the case of the intensive strategy, trees increase the efficiency of fine roots and rhizosphere processes (Leuschner *et al*. 2004; Ostonen *et al*. 2011; Lõhmus *et al*. 2006). In the studied stand, the difference between the soil-root interface and bulk soil microbial activity and diversity was markedly higher than in grey alder stands growing on forest land; the specific root area (SRA; m^2 kg^{-1}) was also significantly bigger (Lõhmus *et al*. 2006) than in natural alder stands. Hence, the low fine root biomass and turnover rate both indicate the significantly greater role of the intensive fine root strategy in the studied grey alder stand.

Furthermore, trees competed fiercely for light at the age of 9–10, as stand density was still rather high. Hence, it was more profitable for a tree to enlarge its above-ground part and operate its fine roots very efficiently in order to survive in a dense stand. At the age of 17 years, stand density, the increment of stem mass and FRE had declined compared to the 10-year-old stand. As suggested in many studies (Björklund and Ferm 1982; Lõhmus *et al*. 1996; Uri *et al*. 2009; Rytter 1995; Rytter *et al*. 2000; Miežite and Dreimanis 2006; etc.), the bulk maturity and optimal rotation length of grey alder fall between the ages 15 to 20. Hence, as the intense and rapid increase of the above-ground part of the stand had dwindled, the FRE of the grey alder fine roots had also declined.

Nitrogen-fixing species, owing to their N_2-fixing ability through microbial symbiosis, can increase soil N and C content. N_2-fixing trees significantly affect the soil C pool by increasing detritus input or humus formation, or by decreasing the rate of decomposition (Binkley 2005). Such species have been widely used as pioneer plants in the recovery of degraded areas (Fisher 1995; Johnson and Curtis 2001). Both the N and C content in the upper soil layer has increased significantly during the growing period of the grey alder stand (Table 1). However, the contribution of fine roots and nodules to the soil N and C increase has been modest due to the constantly low FRB and NB values (Table 4). As N and C concentrations in fine roots and nodules have been at a constant level throughout the study period, the main factors affecting N and C accumulation in soil are FRB and NB.

In our stand, fine root litter formed merely 14% of the total annual tree litter input into soil; the main input of the N and C in grey alder stand comes from leaf litter instead. The total C stock in the soil of the studied stand has significantly increased, which is in good accordance with other studies carried out in short-rotation stands (Liski *et al*. 2001). The effect of alders on the N and C content of soil is significant and fast: the N storage in the upper 10 cm soil layer had increased from 1.40 to 1.72 t ha^{-1}, while the respective increase in C was from 18.2 to 24.3 t ha^{-1}. The average C accumulation in soil during the period 1998–2010 was 0.32 t C ha^{-1} yr^{-1} and average N accumulation 28.3 kg C ha^{-1} yr^{-1}. However, only 0.6 % of the total C input of the tree biomass of the 17-year-old grey alder stand is accumulated in fine roots. Thus, C sequestration into soil via fine roots is much smaller than via the above-ground litter flux.

Conclusions

Grey alder bioproduction is very high at a young age; the species can be considered suitable for SRF. The CAI of grey alder fluctuates greatly, probably depending on weather conditions and the age of the stand. The FRB dynamic in grey alder stand stabilized already at the stand age of 10 years, and in the 17-year-old stand, it had not increased. However, the FRB per tree had increased continuously throughout the stand development due to the natural self-harvesting process and the decreasing number of trees. A strong positive correlation was established between FRB and stand basal area and stem mass. The NB increased during stand development but at the same time, the number of nodules decreased. Grey alder stand affects the N and C status of soil to a great extent;, however, it is mainly affected by the above-ground litter flux. The contribution of fine roots to the sequestration of N or C into soil is modest owing to their small biomass. Due to rapid decomposition, fine root necromass in soil was very small.

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1998 – 2001	Rapla Co-Educational Gymnasium
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	“Renewable energy and energy efficiency”. ITEC training program. TERI, New Delhi, India
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Teaduskraad:

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Teadustöö põhisuunad:

Metsakasvatus, kiirekasvulised lehtpuud, lühikese raieringiga metsandus, toitainete ringed ökosüsteemides, kändude juurimine

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2011 – 2014	Siseriiklik leping 8-2/T11082MIMK: Kuusekändude varumise metsanduslikud aspektid ja kaasnevate keskkonnamõjude hindamine. Põhitäitja
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2007 – 2010	ETF grant nr 7069: Süsiniku akumulatsioon ja puistu kasvukäik arukaasikutes. Põhitäitja
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2006	ETF grant nr 6087: Loomsed häiringud ja nende tagajärjed metsaökosüsteemides. Põhitäitja

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2. Uri V, Varik M, Aosaar J, Kanal A, Kukumägi M, Lõhmus K (2012) Biomass production and carbon sequestration in a fertile silver birch (*Betula pendula* Roth) forest chronosequence. Forest Ecology and Management 267;117-126

3. Aosaar J, Varik M, Lõhmus K, Uri V (2011) Stemwood density in young grey alder (*Alnus incana* (L.) Moench) and Hybrid Alder (*Alnus hybrida* A. Br.) stands growing on abandoned agricultural land. Baltic Forestry 17(2):256-261

4. Uri V, Lõhmus K, Mander Ü, Ostonen I, Aosaar J, Maddisson M, Helmisaari H-S, Augustin J (2011) Long-term effects on nitrogen budget of a short-rotation grey alder (*Alnus incana* (L.) Moench) forest in abandoned agricultural land. Ecological Engineering 37(6):920-930

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1. Kurm M, Aosaar J, Kiviste A (2011) Väetamise mõju hariliku kuuse (*Picea abies* (L.) Karst) poogenditele Pauska seemlas. Metsanduslikud Uurimused / Forestry Studies 54:71-89

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5. Aosaar J, Uri V (2008) Halli lepa, hübriidlepa ja arukase biomassi produktsioon endistel põllumaadel. Metsanduslikud Uurimused / Forestry Studies 48:53-66

6. Aosaar J, Kurm M, Kiviste A (2006) Väetamise mõju kestvuse uurimine hariliku kuuse (*Picea abies* (L.) Karst) poogenditele Pauska seemlas. Metsanduslikud uurimused / Forestry Studies 44:71-84

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1. Aosaar J, Varik M, Uri V (2012) Hall-lepikute muutuv roll Eesti metsanduses. Eesti Loodus 6-7, 29-31

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